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ORIGINAL PAPER

Large mammal ecology in the late Middle Miocene Gratkorn locality (Austria)

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Abstract $\delta^{18}O_{CO3}$, $\delta^{13}C$ and $^{87}Sr/^{86}Sr$ measurements were performed on tooth enamel of several species to gain information on the diet and mobility of herbivorous large mammals from Gratkorn (Austria; late Sarmatian sensu stricto; 12.2–12.0 Ma). Except for the tragulid *Dorcatherium naui*, which was most likely frugivorous to a certain degree, the mean values and the total ranges of $\delta^{13}C$ and $\delta^{18}O$ of the large mammal taxa are typical for an exclusively C_3 vegetation diet and point to predominantly browsing in mesic/woodland environments. Occupation of different ecological niches is indicated by variation in $\delta^{18}O$ and $\delta^{13}C$ among the taxa, and could be shown to be typical for the species by comparison with other Miocene localities from different areas and ages. The small moschid *Micromeryx flourensianus* might have occasionally fed on fruits. The cervid *Euprox furcatus* represents a typical subcanopy browsing taxon. The proboscidean *Deinotherium levius* vel *giganteum* browsed on canopy plants in the higher parts of an exclusively C_3 vegetation as did the bovid *Tethytragus* sp.. Generally higher values for $\delta^{18}O$ and $\delta^{13}C$ of *Lartetotherium sansaniense* indicate feeding in a more open environment. Different ecological niches can be reconstructed for the two suids. While *Listriodon splendens* was a browsing taxon with a considerable input of fruits and maybe some grass in its diet, *Parachleuastochoerus steinheimensis* might have included roots. Distinct differences in $^{87}Sr/^{86}Sr$ values indicate that most of the larger mammals (*Deinotherium levius* vel *giganteum*, *Parachleuastochoerus steinheimensis*, *Euprox furcatus*, *Lartetotherium sansaniense* and to a minor degree maybe *Listriodon splendens*) were not permanent residents of the area around Gratkorn but rather inhabited a wider area, most likely including the Styrian Basin and the higher altitudes of the Eastern Alps' palaeozoic basement.

Keywords Oxygen · Carbon · Strontium · Isotope · Enamel · Diet · Niche partitioning · Central Europe · Paratethys

This article is a contribution to the special issue "The Sarmatian vertebrate locality Gratkorn, Styrian Basin."

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Introduction

The Gratkorn locality (St. Stefan clay pit) is located 10 km NNW of Graz (Styria, Austria). The fossil-bearing palaeosol of late Middle Miocene age (late Sarmatian sensu stricto; 12.2–12.0 Ma; Gross et al. 2011) houses abundant small and large mammal fossils and is one of the richest vertebrate localities (the richest for the Paratethys realm) of this time period recorded so far. All mammalian fossils originate from a single fine-grained clastic soil layer (55 cm in total thickness; Gross et al. 2011; 2014, this issue), interpreted as a floodplain palaeosol (Gross et al. 2011). The uniformity of the palaeosol (without distinct soil horizons), the preservation of vertebrate and invertebrate remains and even coprolites point to a rather rapid accumulation and short time of soil formation (10^1–10^2 years; Gross et al. 2011; Havlik et al. 2014, this issue). Alternating wet and dry periods have been reconstructed based on lithology and fossil content (Gross et al. 2011; 2014, this issue) and on relict bedding, intense mottling, and drab colouring in the upper part of the palaeosol. All these features indicate an increase in hydromorphic conditions from the lower to the upper part of the soil. Due to the fast deposition of the palaeosol and the lack of any indications for reworking of the fossil content (flora and fauna), all the components of the excavated assemblage, including plants and animals, are considered to be contemporaneous and accumulated within a few decades (see also Havlik et al. 2014, this issue for further discussion). Palaeoclimatic reconstructions based on pedogenic features and the faunal composition of ectothermic vertebrates indicate a semi-arid, subtropical climate with distinct seasonality, a mean annual precipitation (MAP) of 486±252 mm, and a mean annual temperature (MAT) of ~15 °C (Gross et al. 2011).

Although scientific analysis of the fossil flora from the Gratkorn locality is still in progress, it can already be said that medium-sized hackberry trees grew frequently in the area due to the high abundance of *Celtis* endocarps, especially in the upper part of the palaeosol. Besides large mammals, a quite diverse ectothermic vertebrate fauna, a few bird remains, and a rich and diverse small mammal fauna (for faunal lists, see Gross et al. 2011; Böhme and Vasilyan 2014, this issue; Göhlich and Gross 2014, this issue; Prieto et al. 2014, this issue) have been excavated at Gratkorn. Herbivorous large mammal taxa are represented by small body sizes of less than 10 kg (Moschidae: *Micromeryx flourensianus* and ?*Hispanomeryx* sp.) up to large species, such as, e.g. the proboscidean *Deinotherium levius* vel *giganteum* (Aiglstorfer et al. 2014a, this issue), and three rhinocerotid species, *Aceratherium* sp., *Brachypotherium brachypus* and *Lartetotherium sansaniense*, which can reach more than 1000 kg in weight (Aiglstorfer et al. 2014b, this issue). Since skeletal material of *Brachypotherium brachypus* comprises only postcranial elements and *Aceratherium* sp. is only represented by a deciduous premolar, isotopic measurements of rhinocerotids could be gained only for *Lartetotherium sansaniense*. The chalicothere *Chalicotherium goldfussi* and the equid *Anchitherium* sp. are further faunal elements of the Gratkorn assemblage (Aiglstorfer et al. 2014b, this issue), but could not be measured due to scarcity of material or total lack of dental material. Suidae are represented in Gratkorn by two species, the more bunodont *Parachleuastochoerus steinheimensis*, and the more lophodont *Listriodon splendens* (van der Made et al. 2014). Ruminants are the most abundant large mammals, and are represented by the cervid *Euprox furcatus* (most frequent species), the tragulid *Dorcatherium naui* (second most frequent species), the above-mentioned two Moschidae, a large palaeomerycid (which is represented only by a single bone), and by the bovid *Tethytragus* sp. (so far recorded with only one individual; Aiglstorfer et al. 2014c, this issue).

Stable isotopes as indicator for ecology

Carbon isotopes

The carbon isotope ratio ($^{12}C/^{13}C$) of vertebrate fossils yields information about the diet and ecology of animals, since differences in isotopic compositions of diet are incorporated into body tissues (DeNiro and Epstein 1978; Tütken and Vennemann 2009; Ecker et al. 2013). Dental enamel proved to be an ideal tissue for this investigation as it is less susceptible to diagenetic alteration than bone or dentine (Koch et al. 1997; Bocherens and Sen 1998; Lee-Thorp and Sponheimer 2003; Tütken et al. 2006; Domingo et al. 2009, 2012; Tütken and Vennemann 2009; Bocherens et al. 2011a).

Plant carbon isotope compositions vary due to different photosynthetic pathways for atmospheric CO_2 assimilation. While today, most trees, shrubs, and "cool-season growing" grasses fix CO_2 by forming a 3-carbon molecule, therefore termed C_3 plants, C_4 plants, representing most of "warm-season growing" grasses and sedges in warm and/or more arid habitats, fix CO_2 in a 4-carbon molecule (Ehleringer and Cerling 2002; Tipple and Pagani 2007). In modern plant tissues, a different $\delta^{13}C$ value is observed for C_3 (−36 to −22 ‰) and C_4 plants (−17 to −9 ‰; Bocherens et al. 1993; Tipple and Pagani 2007; Domingo et al. 2012; all $\delta^{13}C$ and $\delta^{18}O$ values are reported relative to the Vienna Pee Dee Belemnite, V-PDB, standard, if not given otherwise). A third photosynthetic pathway, the crassulacean acid metabolism (CAM; common in desert succulents, tropical epiphytes, and aquatic plants) is characterised by fixation of CO_2 at nighttime. It is rarer (6 % of terrestrial and 6 % of aquatic plants; Keeley and Rundel 2003) and often corresponds to environments in climatically stressful conditions, such as increased aridity (Tütken 2011). Their $\delta^{13}C$ values show a wider range (−30 to −11 ‰) and overlap with values for C_3 and C_4 plants (Tütken 2011). CAM plants usually comprise only a marginal biomass in ecosystems and do not represent the expected food plants for the herbivorous large mammal taxa sampled for this publication.

Herbivores incorporate the ingested plant carbon in their mineralised skeletal and dental tissues, such as bone, dentine and tooth enamel (DeNiro and Epstein 1978; Tütken and Vennemann 2009; Ecker et al. 2013). Carbonate isotope ratios in enamel of herbivores can thus be used to reconstruct the proportion of C_3 or C_4 plants in their diet. An average $\Delta^{13}C_{enamel\text{-}diet}$ enrichment factor of 14.1±0.5 ‰ was observed by Cerling and Harris (1999) for large ruminants (with a total range of 12.6–14.7 ‰). They stated that non-ruminant ungulates give similar values and they did not find a significant difference among taxa. For the sampled rhinocerotids, they observed 14.4±1.6 ‰. In an experiment with controlled diets, Passey et al. (2005) showed that digestive physiology considerably influences the enrichment factor as they measured a factor of 14.6±0.7 ‰ for domestic cattle (ruminant digestion) and a factor of 13.3±0.3 ‰ for pigs (non-ruminant digestion). Since it cannot be estimated whether the digestive physiology of ruminants from Gratkorn is comparable to modern representatives (see differences in digestive physiology of modern Tragulidae and Pecora; Rössner 2007), the average $\Delta^{13}C_{enamel\text{-}diet}$ enrichment factor of 14.1±0.5 ‰ after Cerling and Harris (1999) has been applied to the herbivorous large mammals from Gratkorn, comparable to other works dealing with Miocene herbivorous large mammals (Domingo et al. 2009, 2012; Tütken and Vennemann 2009; Merceron et al. 2013).

In modern large mammal faunas, pure C_3 consumers exhibit a range of −22 to −8 ‰, mixed feeders a range of −8 to −3 ‰, and pure C_4 feeders a range of −3 to +5 ‰ in $\delta^{13}C$ for enamel (Cerling et al. 1997a, b; Domingo et al. 2012). For pure C_3 feeders, Domingo et al. (2012) estimated the ranges for the different habitats, closed canopy (−22 to −16 ‰), mesic/woodland (−16 to −11 ‰) and open/arid (−11 to −8 ‰). However, when dealing with fossil taxa, variations of $\delta^{13}C$ for the atmospheric CO_2 have to be taken into consideration. Modern atmospheric CO_2 ($\delta^{13}C_{CO2}$=−8 ‰) is depleted in ^{13}C compared with preindustrial CO_2 ($\delta^{13}C$= −6.5‰), due to the fossil-fuel burning of ^{12}C-rich hydrocarbons (Friedli et al. 1986). Tipple et al. (2010) reconstructed variations in the $\delta^{13}C$ value of the atmospheric CO_2 for the Cenozoic based on isotopic data derived from benthic foraminifera. Following their measurements, a $\delta^{13}C$ value of about −6 ‰ can be estimated for the latest Middle Miocene CO_2 (12 Ma; 2 ‰ higher than in the modern atmosphere). Late Middle Miocene C_3 feeders are thus expected to have $\delta^{13}C$ values ranging from −20 to −6 ‰, with −20 to −14 ‰ for feeding in closed canopy, −14 to −9 ‰ in mesic/woodland environment, and −9 to −6 ‰ in more open/arid C_3 vegetation. Values between −6 and −1 ‰ and between −1 and +7 ‰ are expected for mixed feeders and pure C_4 feeders, respectively (Domingo et al. 2012).

Although the existence of C_4 grasses has been documented at least for southwestern Europe since the Early Oligocene (Urban et al. 2010), C_3 plants represent the dominant vegetation in Europe during the Miocene and no noteworthy C_4 grasslands evolved until the Late Miocene (Cerling et al. 1993; Tütken and Vennemann 2009). Though small amounts of C_4 vegetation cannot be completely ruled out for the Miocene of Europe, isotopic values measured on Late Miocene *Hippotherium* specimens from Central Europe and herbivorous large mammals from the Iberian Peninsula showed a pure C_3 plant diet for these animals (Domingo et al. 2013; Tütken et al. 2013). The same taxa or closely related ones are known to have consumed C_4 plants when they were available (see Nelson 2007; Badgley et al. 2008; Passey et al. 2009; Bocherens et al. 2011a).

Oxygen Isotopes

Variations in the oxygen isotope ratio ($^{16}O/^{18}O$) in skeletal and dental tissues are in equilibrium with the body water and thus record the in vivo signal of the animal (Longinelli 1984). Oxygen isotope values of the body water are mostly influenced by the composition of the drinking water (meteoric water ($\delta^{18}O_{H2O}$)), and the drinking behaviour of the animal (Longinelli 1984; Luz et al. 1984; Kohn 1996; Kohn et al. 1996; Bocherens et al. 1996; Tütken et al. 2006; Levin et al. 2006; Clementz et al. 2008). While, for example, $\delta^{18}O$ values of terrestrial obligate drinkers mainly depend on the values of the surface water, drought-tolerant species have usually less negative values as they gain more water from leaves, fruits, and seeds, which are more enriched in ^{18}O (Kohn 1996; Kohn et al. 1996). Plant roots and stems usually display similar values as meteoric water (Tütken and Vennemann 2009). In contrast to terrestrial animals, aquatic animals have generally lower values in $\delta^{18}O$ (Bocherens et al. 1996; Clementz et al. 2008). The $\delta^{18}O_{H2O}$ value of meteoric water is influenced by climatic conditions, such as air temperature, degree of aridity (amount of precipitation vs. evaporation), seasonality of precipitation, or the trajectories of storms, as well as by geographic conditions, for example latitude or distance from the source area (continental effect) (Dansgaard 1964; Rozanski et al. 1993; Higgins and MacFadden 2004; Levin et al. 2006). Thus, $\delta^{18}O$ values preserved in fossil enamel help to reconstruct climatic conditions as well as infer information concerning animal ecology. Because tooth mineralisation is a progressive process, variations in climatic conditions can be recorded along the growth axis of the tooth and thus high crowned teeth can give information on seasonal variations (Kohn 2004; MacFadden and Higgins 2004; Nelson 2005; van Dam and Reichert 2009; Zin-Maung-Maung-Thein et al. 2011; Tütken et al. 2013).

The $\delta^{18}O$ value of the ingested water is incorporated in the mineral phase of bones and teeth and mostly bound on phosphate (PO_4^{3-}) and carbonate (CO_3^{2-}) ions, with the greater amount being incorporated in phosphate, as carbonate comprises only 2–4 wt.% of the mineral phase (Tütken and Vennemann 2009). While the PO_4 component is less susceptible to inorganic diagenetic alteration than the CO_3 component, the latter suffers less from microbially-mediated isotopic exchange (Domingo et al. 2013). As the $\delta^{18}O$ values of the phosphate and carbonate components are correlated and exhibit an equilibrium offset of about 8.5 ‰, both are usable for reconstruction of the in vivo signal of animals (Iacumin et al. 1996).

$^{87}Sr/^{86}Sr$: Indicator of migration

In addition to $\delta^{18}O$ and $\delta^{13}C$ values, the strontium isotope composition ($^{87}Sr/^{86}Sr$ ratio) of diet and drinking water is incorporated in the skeletal and dental tissues of animals (Hoppe et al. 1999; Maurer et al. 2012). Since this ratio is constant and does not change up the food chain, it reflects the bioavailable $^{87}Sr/^{86}Sr$ in the animal's habitat (Blum et al. 2000; Bentley 2006). This value depends on the $^{87}Sr/^{86}Sr$ ratios in bioavailable strontium of the underlying bedrocks. The latter is mainly influenced by the primary Rb concentration, respectively the Rb/Sr ratio, as well as the age of the rock (Tütken 2010). Thus, older and Rb-enriched bedrocks display higher $^{87}Sr/^{86}Sr$ ratios (Bentley 2006; Tütken 2010). However, differences from bedrock to bioavailable ratios can be observed for example due to residual clay minerals with higher Rb/Sr and $^{87}Sr/^{86}Sr$ than the underlying bedrock (Cooke et al. 2001; Tütken et al. 2011), complicating the reconstruction of provenance with $^{87}Sr/^{86}Sr$ ratios. In any case the ratio is still related to the underlying rock, though sometimes in a more complex way (Maurer et al. 2012) and thus still enables reconstruction of provenance or possible migration of the animal (Tütken and Vennemann 2009; Maurer et al.

2012). The latter is possible as tooth enamel grows progressively and therefore incorporates variations in isotopic composition, as mentioned above. While large mammals can undertake long-distance migrations (Hoppe et al. 1999; Tütken and Vennemann 2009; Maurer et al. 2012), small mammals and invertebrates display only small individual travel distances (Porder et al. 2003) and are thus more likely to represent the local bioavailable $^{87}Sr/^{86}Sr$ values. Hence, small mammals are often used to determine the local $^{87}Sr/^{86}Sr$ ratios (see Bentley 2006 and references therein).

Institutional Abbreviations

GPIT	Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany
IGM	Montanuniversität Leoben, Leoben, Austria
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
UMJGP	Universalmuseum Joanneum, Graz, Austria

Material

We analysed the carbonate component of 14 bulk enamel samples of large mammal teeth (*Parachleuastochoerus steinheimensis*, *Listriodon splendens*, *Dorcatherium naui*, *Euprox furcatus*, *Micromeryx flourensianus*, *Tethytragus* sp.; see Appendix 1), three bulk samples of whole small mammal teeth (cheek teeth of *Schizogalerix voesendorfensis* and *Prolagus oeningensis* and incisors of indeterminate small mammals) and 21 serial samples of *Deinotherium levius* vel *giganteum* and *Lartetotherium sansaniense* for $\delta^{18}O_{CO3}$ and $\delta^{13}C$. Due to scarcity of material, the second moschid ?*Hispanomeryx* sp. was not measured. To avoid milk suckling and weaning signals, M3s (upper third molars) or m3s (lower third molars) were sampled for large mammals, if possible. Additionally, gastropods (*Pseudidyla martingrossi*, *Limax* sp., *Pleurodonte michalkovaci*, *Testacella schuetti*, and opercula of indetermined gastropods), plant remains (*Celtis* endocarps), soil samples (random and samples from upper and lower parts), and a microbialite (originating from the uppermost part of the palaeosol; see Havlik et al. 2014, this issue for details) were analysed. Strontium isotope composition ($^{87}Sr/^{86}Sr$) was measured on enamel samples of *Listriodon splendens*, *Parachleuastochoerus steinheimensis*, *Dorcatherium naui*, *Euprox furcatus*, *Tethytragus* sp., *Lartetotherium sansaniense*, *Deinotherium levius* vel *giganteum*, *Schizogalerix voesendorfensis*, *Prolagus oeningensis*, *Limax* sp., *Pleurodonte michalkovaci*, and the microbialite from Gratkorn. All material is housed at GPIT and UMJGP.

Large mammal enamel values ($\delta^{18}O_{CO3}$ and $\delta^{13}C_{CO3}$) are compared with values from Middle Miocene localities from Austria, Germany, and Spain.

The following taxa were sampled for direct comparison at the IGM, UMJGP, and NHMW (for detailed information, see Appendix 2):

- *Dorcatherium crassum*, *Dorcatherium vindebonense* (tragulids), and *Hoploaceratherium* sp. (rhinocerotid) from the early Middle Miocene locality of Göriach (Austria; ~14.5 Ma ± 0.3 Ma);
- *Heteroprox larteti* (cervid) and *Prodeinotherium bavaricum* (deinothere) from the early Middle Miocene locality of Seegraben (Austria; 14.8 Ma);
- *Deinotherium* sp. from the late Middle Miocene localities of Türkenschanze (Austria; 12.6 Ma) and Trössing near Gnas (Austria; 12.7–11.6 Ma);
- *Brachypotherium* (?) from Trössing near Gnas;
- *Deinotherium* from the locality of Bruck an der Leitha (Austria; assumably early Sarmatian; 12.7–12.2 Ma) and from the Miocene localities of Wolfau (Austria; early Late Miocene) and Mödling (Austria; Miocene);
- *Brachypotherium* sp. from the Miocene locality of Eichkogel near Mödling (Austria).

Furthermore, comparison data could be gained from the literature for the following taxa and localities:

- Sandelzhausen (Germany; 15.2–15.1 Ma; from Tütken and Vennemann 2009): *Lartetotherium sansaniense*, *Heteroprox eggeri* (cervid), *Gomphotherium subtapiroideum* (proboscidean), *Plesiaceratherium fahlbuschi* and *Prosantorhinus germanicus* (both rhinocerotids);
- Somosaguas (Spain; 14.1–13.8 Ma; from Domingo et al. 2009): *Gomphotherium angustidens* (proboscidean), *Conohyus simorrensis* (suid), and indetermined ruminants;
- Steinheim a. A. (am Albuch; Germany; Middle Miocene; 13.8–13.7 Ma; from Tütken et al. 2006): *Parachleuastochoerus steinheimensis*, *Listriodon splendens*, *Euprox* vel *Heteroprox*, *Micromeryx flourensianus*, *Gomphotherium steinheimense* (proboscidean), *Lartetotherium sansaniense*, *Brachypotherium brachypus*, *Alicornops simorrensis* (rhinocerotid) and *Aceratherium* sp.;
- Paracuellos 5 (Spain; Middle Miocene; 13.7–13.6 Ma; from Domingo et al. 2012): *Gomphotherium angustidens*, *Listriodon splendens*;
- Puente de Vallecas (Spain; Middle Miocene; 13.7–13.6 Ma; from Domingo et al. 2012): *Heteroprox moralesi* (cervid);
- Paracuellos 3 (Spain; Middle Miocene; 13.4–13.0 Ma; from Domingo et al. 2012): *Listriodon splendens* and *Tethytragus langai* (bovid).

Methods

C and O isotope measurements of the carbonate component of hydroxyapatite

Samples were obtained by hand drilling with a diamond-tipped dental burr on Dremel 10.8 V and Emax EVOlution and by crushing with a steel mortar and pestle. Prior to enamel sampling, the outer surface of the teeth was abraded by hand drilling to minimise effects of diagenetic alteration. Invertebrate samples were optically checked for contamination and cleaned with deionized water prior to crushing. Parts with stronger coloration and visible cracks were avoided to minimise contamination. Isotope analysis was done using 5–15 mg (depending on tooth size and fragility) enamel powder. Prior to analysis of carbon and oxygen isotopes, all enamel and dentine samples were chemically pretreated with 2 % NaOCl (24 h) and 0.1 M Ca-Acetate acetic acid buffer solution (24 h) in order to remove organics and diagenetic carbonate (Bocherens et al. 1996). Soil samples, invertebrates, and microbialite were pretreated with 2 % NaOCl (24 h). Samples were rinsed with deionised water after each chemical treatment. About 2–3 mg of powder were used for C and O analyses and measurement of $CaCO_3$ content (wt. %; ± 10 %). This was performed at 70 °C with a Gasbench II connected to a Finnigan MAT 252 gas mass spectrometer, at the Department of Geosciences of the University of Tübingen (Germany). The measured O and C isotopic compositions were calibrated using the standards NBS-18 ($\delta^{18}O=-22.96$ ‰, $\delta^{13}C=-5.00$ ‰ V-PDB) and the NBS-19 ($\delta^{18}O=-2.20$ ‰, $\delta^{13}C=1.95$ ‰ V-PDB), with a reproducibility of ±0.1 ‰ ($\delta^{13}C$) and ±0.2 ‰ ($\delta^{18}O$). Following Bocherens et al. (2011b), isotopic measurements are expressed as δ (delta) values in ‰, as follows: $\delta^{Y}X=(\text{Rsample}/\text{Rstandard}-1)\times 1{,}000$, where X is C or O and Y is the mass number 13 or 18, and R is the isotopic ratio $^{13}C/^{12}C$ and $^{18}O/^{16}O$, respectively. The δ values are quoted in reference to international standards: Vienna Pee Dee Belemnite (V-PDB) for carbon and oxygen, furthermore, for oxygen Vienna Standard Mean Ocean Water (V-SMOW). In general, if not noted otherwise, V-PDB values are used. If $\delta^{18}O$ values measured in V-PDB were converted to V-SMOW, this was accomplished using the following formula: $\delta^{18}O\ (\text{V-SMOW})=[\delta^{18}O\ (\text{V-PDB})\times 1.03086]+30.86$.

Due to the small number of samples, maximum and minimum values are given in figures instead of standard deviations. Accordingly, to allow comparison, literature data are plotted with mean values and total ranges instead of standard deviations.

$^{87}Sr/^{86}Sr$ of the carbonate in the hydroxyapatite

A representative amount of the samples analysed for C and O was selected for $^{87}Sr/^{86}Sr$ analysis. Furthermore, three samples of each of the serially sampled teeth of *Lartetotherium sansaniense* and *Deinotherium levius* vel *giganteum* (where possible maxima and minima in $\delta^{18}O$) were chosen. For $^{87}Sr/^{86}Sr$ analysis, 1–10 mg of pretreated enamel powder were prepared in a clean laboratory. Isotope ratio measurements were performed on the Finnigan MAT 262 TIMS located at the Isotope Geochemistry Group of the University of Tübingen (Germany). Sample material was weighed into Savillex® Teflon beakers, dissolved with 0.5 ml $HCl_{conc.}$ in closed beakers on a hot plate at 80 °C overnight and subsequently dried down. Samples were then redissolved in 2.5 M HCl for the separation of Sr by conventional ion exchange chromatography using quartz glass columns filled with BioRad AG 50 W-X12 (200–400 mesh). Subsequent purification of Sr was achieved in microcolumns filled with Eichrom® Sr-spec resin using the HNO_3–H_2O technique. Sr separates were loaded with a Ta-activator on Re single filaments and isotope ratio measurements were performed in dynamic mode. Analytical mass fractionation was corrected using a $^{88}Sr/^{86}Sr$ ratio of 8.375209 and exponential law. External reproducibility for NBS SRM 987 ($n=18$) is 0.710254±20 (2sd) for the $^{87}Sr/^{86}Sr$ ratio. Total procedural blank (chemistry and loading) was <1,475 pg contributing <1.5 % to the total Sr and thus negligible.

Results and discussion

Sediment, plant, and invertebrate fossils

Sediment samples from different parts of the palaeosol were measured as an indicator for the degree of alteration in dentine and bone of mammals. The samples showed a very wide range for both $\delta^{18}O$ and $\delta^{13}C$ (Fig. 1), probably originating from the strong heterogeneity of the different components of the clastic sediment with little carbonate cement. Similar discrepancies between sediment and diagenetically altered dentine were observed recently for the locality of Höwenegg (Tütken et al. 2013, supplementary data). Furthermore, the low $CaCO_3$ content (0.08–0.46 wt.%; Appendix 1) hinders reliable measurements. The microbialite shows lower values for $\delta^{13}C$ in comparison to the upper part of the palaeosol, representing its host sediment. As biological fractionation produces such negative shifts (Breitbart et al. 2009), the values tentatively confirm the assumption of biogenic (bacterial) build up (see also Havlik et al. 2014, this issue).

Due to assumed strong diagenetic alteration (bad preservation already optically observable; soft, crumbly, high porosity, and rich brownish colour), *Celtis* endocarps were also measured for $\delta^{18}O$ and $\delta^{13}C$ to be used as an indicator for the degree of alteration in dentine and bone of mammals. The endocarps showed the highest $\delta^{18}O$ values measured for the locality and were clearly distinct from all values measured for large and small mammals (Fig. 1). As diagenetic alteration can be a long-term process and even REE uptake does not necessarily have to be restricted to early diagenesis (Herwartz et al. 2011 and 2013), these high values in *Celtis* endocarps could be explained by later (perhaps modern)

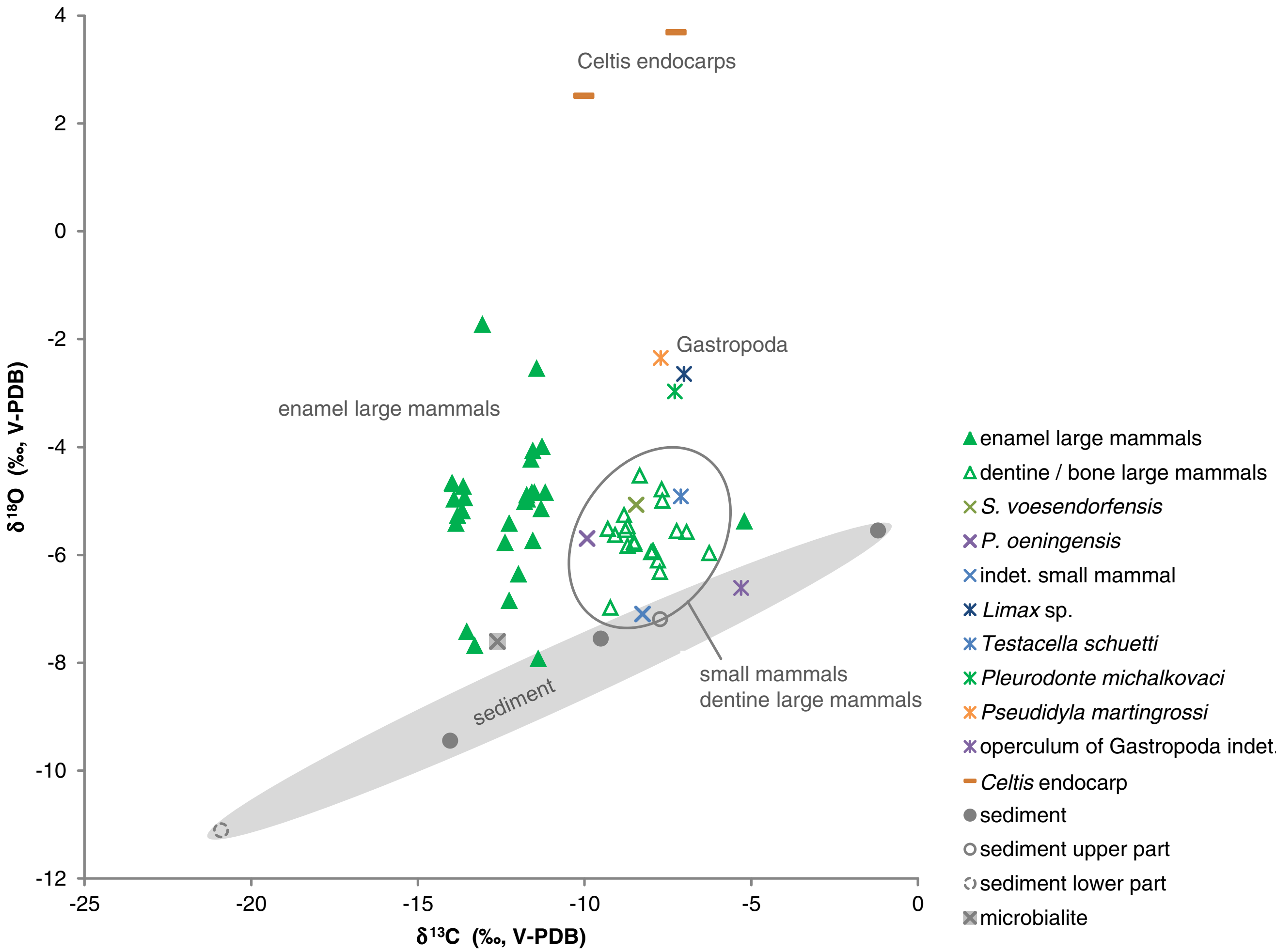

Fig. 1 $\delta^{18}O_{CO3}$ (‰ V-PDB) versus $\delta^{13}C$ (‰ V-PDB) for large mammals (enamel, dentine and bone), small mammals (complete teeth), terrestrial gastropods, *Celtis* endocarps, sediment samples and a microbialite from the Gratkorn locality

diagenetic alteration, to which the fruits are more susceptible as they represent a system more easily accessible for diagenetic fluids due to their bad preservation and higher porosity.

Recrystallisation of gastropod shells of *Pseudidyla martingrossi* and *Pleurodonte michalkovaci* during diagenesis is unlikely as they still possess an aragonitic shell composition (Havlik et al. 2014, this issue). Rudimental shells of the slug *Limax* sp. showed calcite crystals. As the mineralogy of extant species of *Limax* is not fully understood, it cannot be verified whether or not the slug shells from Gratkorn are recrystallised (Havlik et al. 2014, this issue). Therefore, $\delta^{18}O$ and $\delta^{13}C$ values of *Pseudidyla martingrossi* and *Pleurodonte michalkovaci* are considered more reliable in preservation of the in vivo signals. *Pseudidyla martingrossi*, *Pleurodonte michalkovaci*, and *Limax* sp. showed similar $\delta^{18}O$ and $\delta^{13}C$ values, but distinctly higher $\delta^{18}O$ than small mammal whole teeth, large mammal dentine, other gastropod remains (*Testacella schuetti*, opercula of indeterminate gastropod), and sediment (Fig. 1). As little isotopic exchange can be assumed for the non-recrystallised *Pseudidyla martingrossi* and *Pleurodonte michalkovaci*, and the values clearly differ from tissues affected by diagenetic alteration (small mammal whole teeth and large mammal dentine), the values for *Pseudidyla martingrossi*, *Pleurodonte michalkovaci*, and *Limax* sp. are considered in vivo signals and fit well with the observations of Yapp (1979), who showed that modern land snails are enriched in ^{18}O in comparison to meteoric water. As point and interval of time of gastropod shell mineralisation depends on many climate variables, for example, seasonality (Yanes et al. 2009), more measurements and a reliable correlation in behaviour and habitat to modern relatives is needed to gain further information. Food preference in terms of C_3 and C_4 plant diet also cannot be easily reconstructed, due for example to changes in metabolic rates (Balakrishnan and Yapp 2004).

Preservation of vertebrate remains

For small mammals, only bulk samples of enamel and dentine could be gained due to the thin enamel cover in comparison to large mammals. The authors are well aware that small mammal $\delta^{13}C$ and $\delta^{18}O_{CO3}$ values are more likely to be significantly biased by diagenetic alteration. The measured small mammal values are therefore not used here for ecological interpretations, but as indicators for diagenetic alteration of bone and dentine of large mammals. Small mammal $\delta^{13}C$ and $\delta^{18}O_{CO3}$ values are well in accordance with bone and dentine of large mammals. Most likely both suffered from stronger isotopic exchange during their early taphonomic history, as is also indicated by the stronger influence of early diagenesis on the REE pattern (Trueman et al. 2006; Trueman 2013; for discussion, see also Havlik et al. 2014, this issue). $^{87}Sr/^{86}Sr$ ratios of small mammals are well suited to reconstruct the local $^{87}Sr/^{86}Sr$ ratios in bioavailable strontium during formation of the palaeosol.

The total carbonate content in large mammal enamel sampled for this work ranged between 4 and 6 % (Appendix 1) for all measured samples and thus presented the same proportions as expected in fresh, unaltered ungulate enamel (Rink and Schwarcz 1995; Julien et al. 2012). Hence, there are no signs of recrystallisation that would have led to unusually low carbonate values or of contamination by exogenous carbonate, which would be indicated by high values (Koch et al. 1997; Ecker et al. 2013). Furthermore, $CaCO_3$ content did not show any correlation with either $\delta^{18}O$ or $\delta^{13}C$ values in the measured samples. Moreover, large mammal enamel $\delta^{18}O$ and $\delta^{13}C$ values are distinct from corresponding measurements of dentine and bone, which clearly overlap with small mammals and invertebrates (Fig. 1), indicating to a certain degree a diagenetic alteration of dentine and bone.

Total REE contents (Havlik et al. 2014, this issue) of vertebrate enamel range from below detection limit (0.07 ppm) up to 284 ppm comprising in general lower values than bone (values between 988 and 13,484 ppm) and dentine (values between 4 and 12,510 ppm). Except for two higher values in ruminants, *Tethytragus* sp. (GPIT/MA/2753: 172.34 ppm) and *Euprox furcatus* (GPIT/MA/2414: 284.42 ppm), enamel REE values were below 30 ppm and therefore indicate that tooth enamel from Gratkorn was not affected by extensive diagenetic alteration (see also discussions in Domingo et al. 2009; Havlik et al. 2014, this issue). The higher values for the two ruminant specimens could be explained by the enamel of ruminants being much thinner and more fragile and therefore more susceptible to diagenetic alteration in comparison to Rhinocerotidae and Deinotheriidae. In the case of *Euprox furcatus* (GPIT/MA/2414), the sampled tooth is a non-erupted molar and thus incomplete mineralisation could explain a higher degree of REE uptake. An incisor of a small mammal with very thin enamel (REE content of 0.079 ppm) and another ruminant, *Dorcatherium naui* (REE content of 0.5281 ppm), showed only small total REE contents. Diagenetic alteration and REE uptake thus seems to be more complex, as also observed by Herwartz et al. (2013). Due to a clear distinction of enamel and dentine/bone values for all measured *Euprox furcatus* and *Tethytragus* sp. and the inconspicuous carbonate content, enamel samples measured from these species are still considered to have retained biogenic $\delta^{18}O$ and $\delta^{13}C$ values.

In general, values of $\delta^{18}O_{CO3}$ have to be considered less reliable than $\delta^{13}C$ values. Two teeth of one individual of *Dorcatherium naui* (UMJGP 204662, m3 dex. and UMJGP 204665, m3 sin.) yielded a difference of 1.15 ‰ for $\delta^{18}O_{CO3}$, while the offset in $\delta^{13}C$ was only 0.03 ‰. As teeth of Middle Miocene ruminants are smaller and possess thinner enamel than, e.g. Late Miocene bovids or than proboscideans, teeth cannot always be sampled at exactly the same tooth element in order to gain the necessary sample amount. The offset of $^{18}O_{CO3}$ might thus result from a different amount of powder from trigonid or talonid and therefore average different mineralisation phases (see, e.g. different mineralisation phases for different conids in Avishai et al. 2004).

Diet of large mammals ($\delta^{18}O$ and $\delta^{13}C$)

Except for the tragulid *Dorcatherium naui* ($\delta^{13}C$: min −11.8 ‰, mean −9.9 ‰, max −5.2 ‰), which was most likely a frugivore to a certain degree, the $\delta^{13}C$ values of enamel of the other herbivorous large mammal teeth displayed a range from −14 to −11.2 ‰ and a mean value of −12.4 ‰ (Fig. 2). They are well within the range of Miocene large mammalian herbivores predominantly feeding in a mesic/woodland environment of a pure C_3 ecosystem, where a range from −14 to −9 ‰ is expected (Domingo et al. 2012). None of the taxa derived its diet from closed-canopy conditions, as Miocene herbivores feeding in closed canopy conditions should have $\delta^{13}C$ values lower than −15/−14 ‰ (Tütken and Vennemann 2009; Domingo et al. 2012). Different values for $\delta^{18}O$ and $\delta^{13}C$ indicate different ecological niches among the large mammals from Gratkorn. The data fit well with a late Middle Miocene faunal assemblage from this area and are well in accordance with other Middle Miocene large mammal communities from Europe (see, e.g. Tütken et al. 2006; Tütken and Vennemann 2009; Domingo et al. 2009, 2012).

Ruminantia

Euprox furcatus

The cervid *Euprox furcatus* generally shows lower values for $\delta^{13}C$ (min: -13.6 ‰, mean: −12.9 ‰, max: −12 ‰; $n=5$) and $\delta^{18}O$ (min: −7.7 ‰, mean: -6.7 ‰, max: −5 ‰; $n=5$) in comparison to other taxa from Gratkorn, overlapping with the values of *M. flourensianus* and the lower value of *Listriodon splendens* (Fig. 2). The $\delta^{13}C$ values of *Euprox furcatus* fit well with feeding in a more closed, forested C_3 environment, and the lower values for both $\delta^{13}C$ and $\delta^{18}O$ to an ecological niche comprising mostly subcanopy diet. Besides inhabiting an environment with less evaporation, the low $\delta^{18}O$ values for *Euprox furcatus* in comparison to other large mammals could also indicate an obligate drinking behaviour (Kohn 1996; Kohn et al. 1996). So far, no isotopic measurements have been carried out on well-determined material of *Euprox furcatus*. The Middle Miocene locality of Steinheim, while yielding rich material of the species, also houses, besides *Euprox furcatus*, a similar-sized cervid, *Heteroprox larteti*,

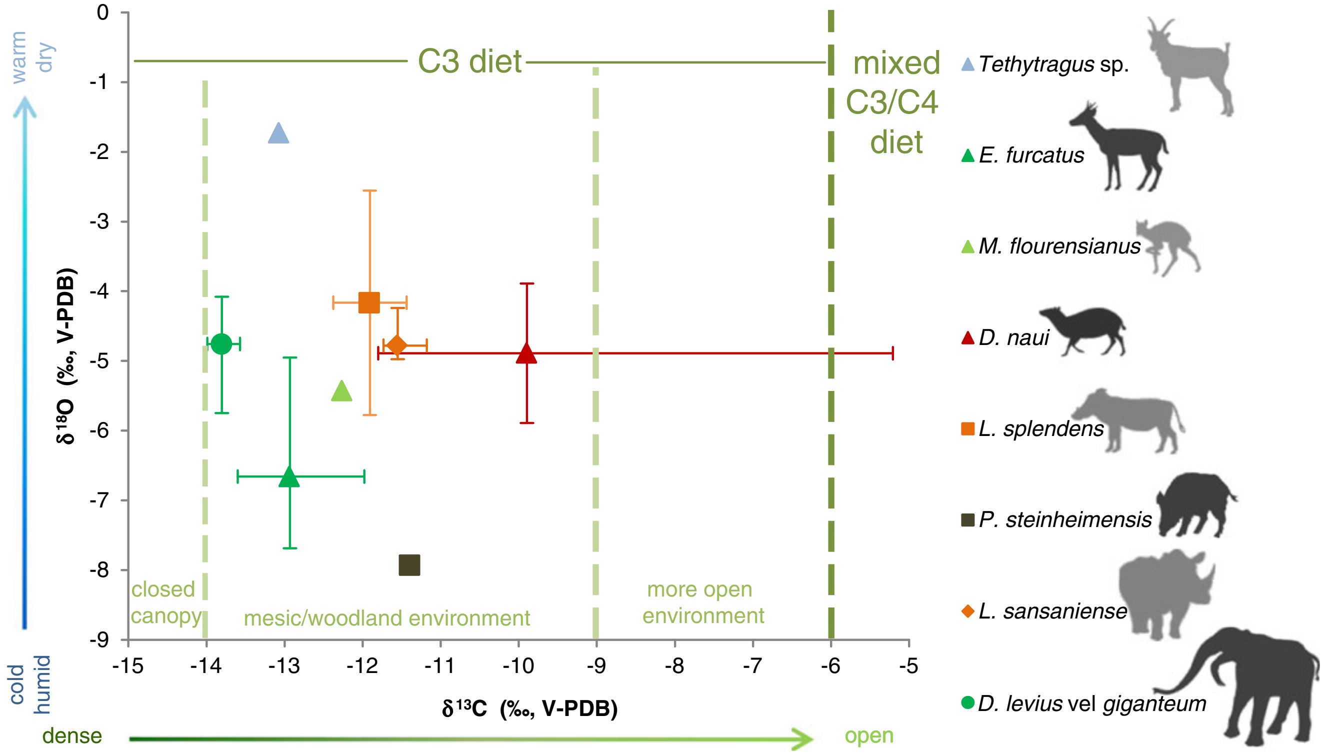

Fig. 2 Mean values with total range of $\delta^{18}O_{CO3}$ (‰ V-PDB) versus $\delta^{13}C$ (‰ V-PDB) for large mammals (enamel) from the Gratkorn locality with designated niches (after Domingo et al. 2012) in a predominantly C_3 vegetation. Trends from dense and cold/humid environment to more open and warm/dry environment are indicated

which cannot be distinguished from the former on isolated dental material alone, and thus isotopic investigations on the locality only allowed a measurement of mixed material (*Euprox* vel *Heteroprox*; Tütken et al. 2006). Comparing measurements of the genus *Heteroprox* and indeterminate ruminants from other localities (Sandelzhausen, Seegraben, Somosaguas, and Puente de Vallecas; data from Tütken et al. 2006; Domingo et al. 2009, 2012; and own measurements) with the data from Gratkorn (Fig. 3a), it can be observed that *Euprox furcatus* shows the lowest values, while *Heteroprox* seems to be more enriched in both ^{18}O and ^{13}C. This could be explained by less browsing in subcanopy environment by the latter in comparison to *Euprox furcatus* but a higher degree of mixed feeding. Merceron et al. (2012) also observed a high degree of grazing in *Heteroprox* from Austria and Slovakia. However, occupation of different ecological niches is also dependent on the ecological conditions and the number of co-occurring species, as was shown in the study of DeMiguel et al. (2011) on the microwear of ruminants in Middle Miocene deposits of Central Spain. This might also explain the classification of *Heteroprox larteti* as a browser in Middle Miocene localities from the NAFB (North Alpine Foreland Basin; Kaiser and Rössner 2007), as it co-occurred with another cervid, *Dicrocerus elegans*, which was classified in their investigation as a mixed feeder. Although a certain degree of variability concerning the degree of mixed feeding in different ruminant assemblages can be expected, DeMiguel et al. (2011) observed a higher intake of grass and tough vegetation in *Heteroprox larteti* than in *Euprox furcatus* at a locality where both co-occurred. So far, there is not enough data to define clearly distinct ecological niches for *Euprox furcatus* (subcanopy browser) and *Heteroprox* ssp. (more open environment mixed feeder). However, the results from Gratkorn and literature data (Tütken et al. 2006; DeMiguel et al. 2011; Domingo et al. 2012), indicate that the interpretation of *Euprox furcatus* as an inhabitant of drier environments by Thenius (1950) is less likely. *Euprox furcatus* rather represents a subcanopy browser and, in the case of co-occurrence with *Heteroprox larteti*, might have displayed a lower degree of mixed feeding than the latter.

Micromeryx flourensianus

A pure C_3 browsing diet can be assumed for the small moschid *Micromeryx flourensianus* ($\delta^{13}C=-12.3$ ‰; $\delta^{18}O=-5.4$ ‰; Fig. 2), possibly with slight enrichment by fruits and seeds, resulting in the slightly higher values for $\delta^{13}C$ and $\delta^{18}O$ in comparison to most of the cervids (Tütken and Vennemann 2009). However, because the isotopic data of *Micromeryx flourensianus* from Gratkorn were measured on only one individual, speculations on diet are rather limited. Merceron et al. (2007) and Merceron (2009) reconstructed a browsing diet (with some affinities to mixed feeding) with a significant intake of fruits and seeds for *Micromeryx*

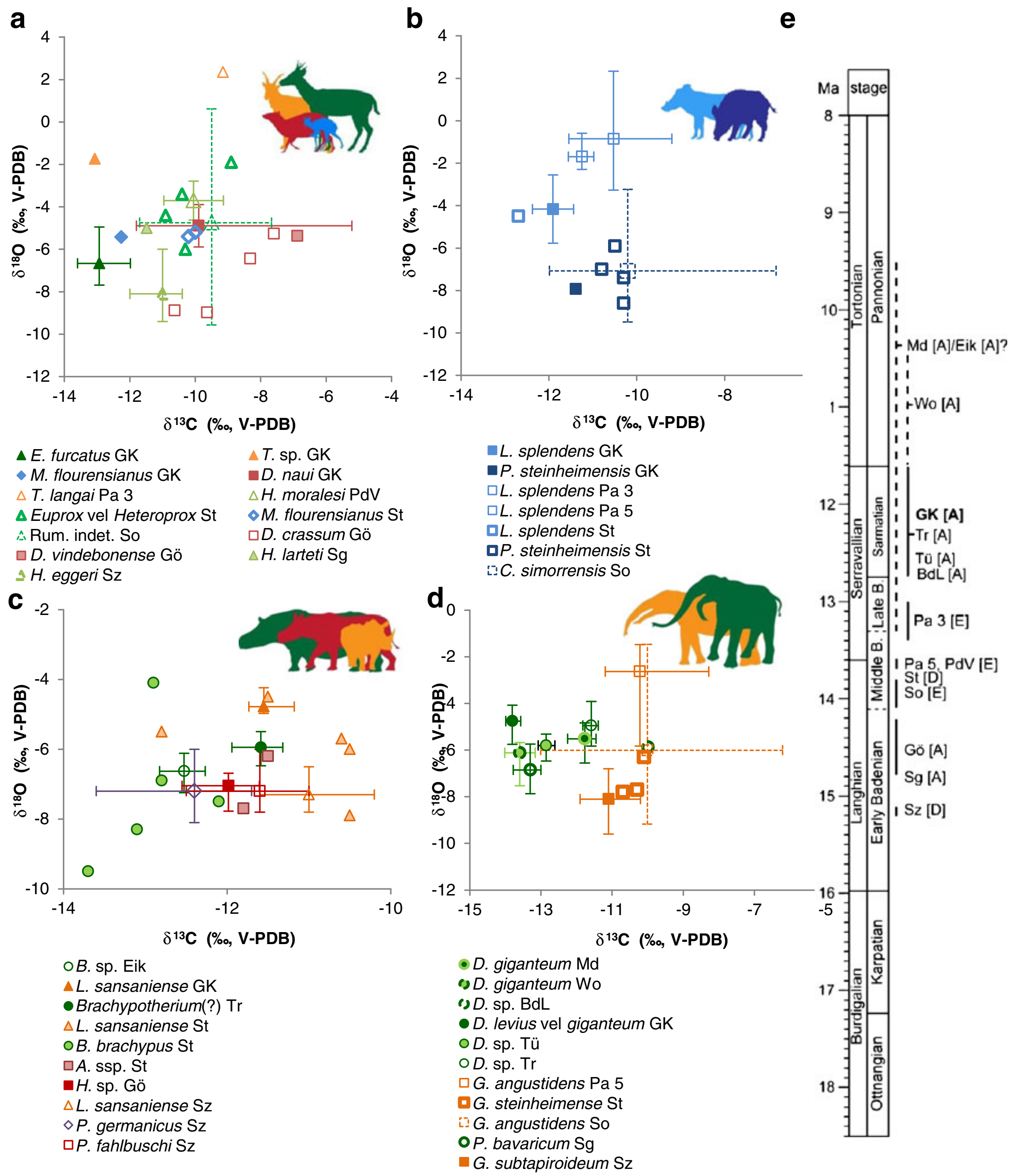

Fig. 3 Mean values with total range of $\delta^{18}O_{CO3}$ (‰ V-PDB) versus $\delta^{13}C$ (‰ V-PDB) for large mammals (enamel) from the Gratkorn locality in comparison with data from other Miocene localities (*GK* Gratkorn (own measurements); *Pa 3* Paracuellos 3 (from Domingo et al. 2012); *PDV* Puente de Vallecas (from Domingo et al. 2012); *St* Steinheim a. A. (from Tütken et al. 2006); *So* Somosaguas (from Domingo et al. 2009); *Gö* Göriach (own measurements); *Sg* Seegraben (own measurements); *Sz* Sandelzhausen (from Tütken and Vennemann 2009); *Pa 5* Paracuellos 5 (from Domingo et al. 2012); *Eik* Eichkogel (own measurement); *Tr* Trössing (own measurements); *Md* Mödling (own measurements); *Wo* Wolfau (own measurements); *BdL* Bruck an der Leitha (own measurements)). **a** Ruminantia (*E. Euprox*; *T. Tethytragus*; *M. Micromeryx*; *D. Dorcatherium*; *H. Heteroprox*; Rum. Ruminantia); **b** Suidae (*L. Listriodon*; *P. Parachleuastochoerus*; *C. Conohyus*); **c** Rhinocerotidae (*B. Brachypotherium*; *L. Lartetotherium*; *A. Aceratherium*; ssp. several species; *H. Hoploaceratherium*; *P. germanicus Prosantorhinus germanicus*; *P. fahlbuschi Plesiaceratherium fahlbuschi*); **d** Proboscidea (*D. Deinotherium*; *G. Gomphotherium*; *P. Prodeinotherium*); **e** Stratigraphic age of different localities (*A* Austria, *D* Germany, *E* Spain, *B* Badenian)

flourensianus from Rudabanya and Atzelsdorf (both Late Miocene). Isotopic data for *Micromeryx flourensianus* from Steinheim (Tütken et al. 2006) are well in accordance with the measurements from Gratkorn (even more enriched in ^{13}C; Fig. 3a). So far, isotopic data and microwear therefore indicate a generally C_3 browsing diet for the small moschid *Micromeryx flourensianus* with considerable intake of fruits or seeds and occasional grazing.

Tethytragus sp.

With a $\delta^{13}C$ value of −13.1 ‰, a pure C_3 browsing diet can be assumed for *Tethytragus* sp.. It shows the highest value for $\delta^{18}O$ (−1.7 ‰) observed in the large mammal fauna of the locality (Fig. 2). In spite of the high REE content in this sample, and the fact that the CO_3 component is more susceptible to diagenetic alteration, the value is still considered to reflect a biological signal. The $CaCO_3$ content is not significantly higher than in other samples recorded, and the $\delta^{18}O$ value is not shifted in the direction of dentine and sediment samples, as would be expected when a considerable bias through diagenetic alteration has occurred. The higher values for $\delta^{18}O$ but similar values for $\delta^{13}C$ in comparison with other ruminants from Gratkorn could result from feeding on top canopy plants exposed to higher evaporation, as was reconstructed, for example, for *Giraffokeryx* (Giraffidae) from Paşalar by Bocherens and Sen (1998) or for *Germanomeryx* (Palaeomerycidae) from Sandelzhausen by Tütken and Vennemann (2009). Other isotopic measurements for the same genus (Domingo et al. 2012) also showed high $\delta^{18}O$ values and are well in accordance with the data from Gratkorn (Fig. 3a). Although small in body size in comparison to *Giraffokeryx* and *Germanomeryx*, feeding on top canopy plants could have been possible for *Tethytragus* due to a caprine-like postcranial adaptation enabling climbing and tree-/rock-jumping to a certain degree (for further discussion, see Aiglstorfer et al. 2014c, this issue). Köhler (1993) could show adaptation to mountainous areas for *Tethytragus koehlerae* from the Turkish locality of Çandir (Middle Miocene). Micro- and mesowear analysis on *Tethytragus* from the Middle Miocene of Central Spain display different degrees of mixed feeding and grazing in their diet and even inconsistency between the two different methods in one population was observed (DeMiguel et al. 2011). As microwear is affected by the so-called "last-supper-effect" (Grine 1986), the diet of *Tethytragus koehlerae* might also depend on seasonal variations, which could also have been the case at Gratkorn.

Dorcatherium naui

So far, no isotopic measurements have been published on Miocene Tragulidae of Europe. The high $\delta^{13}C$ values of −11.8 to −5.2 ‰ with a mean of −9.9 ‰ (n=4) for the tragulid *Dorcatherium naui* were thus quite unexpected, as modern Tragulidae inhabit the undergrowth of forested environments (Rössner 2007), and other species of the genus, like *Dorcatherium crassum*, have been considered as indicators for wetland conditions. Therefore, one would have expected $\delta^{13}C$ and $\delta^{18}O$ values typical for closed canopy or at least subcanopy feeding in a more humid environment for *Dorcatherium naui* from Gratkorn. In contrast to this expectation, this taxon yielded $\delta^{13}C$ values clearly higher than for all other large mammals from the locality (Fig. 2). $\delta^{18}O$ values are instead only slightly higher than in cervids (min: −5.4 ‰, mean: −4.9 ‰, max: −4 ‰). These values can be explained by a certain amount of mixed feeding (leaves and grass) or by ingestion of a considerable amount of fruit. In investigations on a modern large mammal assemblage from the Ituri Forest (Democratic Republic of Congo), tragulids showed higher values for $\delta^{13}C$ but similar ones for $\delta^{18}O$, and nested well within canopy frugivores (Cerling et al. 2004). Moreover, Codron et al. (2005) could show that tree fruits were significantly ^{13}C-enriched, by about 1.5–2 ‰ on average, compared to tree leaves. The mean enrichment of 3 ‰ for $\delta^{13}C$ observed at Gratkorn is slightly higher but would still fit well with the ingestion of a considerable amount of fruit by *Dorcatherium naui*. However, an exclusively frugivore diet for the species cannot be assumed, as the climate (seasonality, MAP of 486±252 mm, and MAT of ~15 °C; Gross et al. 2011) makes an all-year fruit supply for the area around Gratkorn most unlikely. Today, the fruit supply is not high enough even in evergreen forests for a strictly frugivore feeding of terrestrial frugivores all year (Smythe 1986). The assumption of Sponheimer and Lee-Thorp (2001) that frugivores should be more depleted in ^{18}O than folivores can only be sustained under the presumption that the animals fed from the same plant/tree, since besides intraspecific differences (leaves vs. fruits), interspecific differences were also observed in the enrichment in ^{18}O by Dunbar and Wilson (1983). As it is most likely that the leaf-browsing cervid *Euprox furcatus* and the browsing and facultative frugivorous tragulid *Dorcatherium naui* did not feed exclusively on the same plants, the different values in $\delta^{13}C$ and the similar values in $\delta^{18}O$ fit well with the proposed differences in ecological niches. Measurements on other species of the genus, *D. crassum* and *D. vindebonense*, from an intramontane basin (early Middle Miocene locality of Göriach; Austria; ~14.5 Ma ± 0.3 Ma) also showed generally slightly higher $\delta^{13}C$ values than other ruminants (Fig. 3a), which could also result from ingestion of a considerable amount of fruits. Furthermore, works based on microwear analyses reconstructed a frugivore browsing diet for *D. naui* from the Late Miocene locality of Atzelsdorf (Austria; 11.1 Ma; Merceron 2009) and for *Dorcatherium crassum* from Göriach and other Austrian intramontane basins (Merceron et al. 2012), while *Dorcatherium vindebonense* was termed a generalist, comparable to the modern red deer by Merceron et al. (2012). As we cannot exclude a certain amount of mixed feeding (browsing and grazing on C_3 vegetation) from our measurements at the locality of Göriach, and as $\delta^{18}O$ values of the different specimens from the locality show quite a wide range, occupation of more diverse ecological niches among the different *Dorcatherium* specimens with a considerable amount of C_3 grass ingestion do not seem unlikely.

Since there is so far no evidence for the existence of a relevant amount of grass in the vegetation of Gratkorn, and keeping in mind the observations of Merceron (2009), we assume fruit ingestion rather than grazing to be more likely for *Dorcatherium naui* from Gratkorn. In addition, the morphology of the species' incisor arcade rather points to ingestion of fruits to a certain degree more than to grazing (for further discussion, see Aiglstorfer et al. 2014c, this issue). On the other hand, a mixed diet was reconstructed for *Dorcatherium guntianum* from the NAFB by Kaiser and Rössner (2007). It is, together with *Dorcatherium naui*, part of a phylogenetic lineage differing from the more bunodont *Dorcatherium crassum* by more selenodont and higher crowned teeth (for further discussion, see Aiglstorfer et al. 2014c, this issue). Ungar et al. (2012) also observed mixed feeding for Early Miocene Tragulidae from Africa. In summary, for the moment, we therefore consider *Dorcatherium naui* from Gratkorn a browser with facultative frugivory, but we cannot completely rule out a certain amount of mixed feeding.

In addition to different diets, different digestion systems between *Dorcatherium* and higher ruminants could also explain differences in isotopic ratios. In modern tragulids, for example, the rumen, where fermentation takes place in symbiosis with bacteria, is relatively small compared to more derived ruminants (Rössner 2007). Slightly higher δ^{18}O values could furthermore be triggered by less dependency on drinking than observed in the obligate drinker *Euprox furcatus*. Modern tragulids have the lowest water intake of modern ruminants in the tropics (Rössner 2007).

Suidae

Listriodon splendens (min: −12.4 ‰, mean: −11.9 ‰, max: −11.4 ‰; n=2) and *Parachleuastochoerus steinheimensis* (−11.4 ‰) show similar values for δ^{13}C, well in accordance with other browsing taxa. In contrast to δ^{13}C, δ^{18}O values of *Listriodon splendens* (min: −5.8 ‰, mean: −4.2 ‰, max: −2.6 ‰; n=2) and of *Parachleuastochoerus steinheimensis* (−7.9 ‰) are quite distinct (Fig. 2). Because of the Tapir-like lophodont dentition, *Listriodon splendens* has been traditionally considered a specialised folivore (van der Made 1996). Isotopic measurements from Gratkorn fit well within this ecological niche and higher values in δ^{18}O indicate a certain amount of mixed feeding or ingestion of maybe upper canopy fruit, more enriched in ^{18}O (Nelson 2007). This is well in accordance with ecological interpretations based on morphology by van der Made et al. (2014). The distinctly lower δ^{18}O values, but similar δ^{13}C values in *Parachleuastochoerus steinheimensis* from Gratkorn, could be explained by digging for roots, as these are depleted in δ^{18}O in comparison to leaves, while δ^{13}C values are similar (Sponheimer and Lee-Thorp 2001). While incisor and general jaw morphology makes consumption of roots for the genus *Listriodon* unlikely (van der Made 1996 and references therein; van der Made et al. 2014), for the subfamily Tetraconodontinae, to which *Parachleuastochoerus* is assigned, a certain amount of root consumption is assumed due to dental morphology (Hünermann 1999; van der Made et al. 2014). Comparing isotopic measurements from Gratkorn with literature data from other Miocene localities (Tütken et al. 2006; Domingo et al. 2009, 2012; Fig. 3b) different ecological niches for *Listriodon splendens* and for tetraconodontid suids (*Parachleuastochoerus steinheimense* and *Conohyus simorrensis*) are verified and seem to be rather independent from climate and stratigraphic level. While *Listriodon splendens* plots well in a mostly browsing diet with occasional input of fruits or grass, δ^{18}O values in tetraconodontid suids are usually more negative, indicating a considerable amount of rooting in their diet.

Perissodactyla

Lartetotherium sansaniense

The δ^{13}C values of the rhinocerotid *Lartetotherium sansaniense* (min: −11.7 ‰, mean: −11.6 ‰, max: −11.2 ‰) are slightly higher than in the cervid *Euprox furcatus* or the proboscidean *Deinotherium*, though still nesting well within the range expected for feeding in a mesic/woodland C_3-dominated environment (Fig. 2). Tütken et al. (2006) and Tütken and Vennemann (2009) observed higher δ^{13}C values for *Lartetotherium sansaniense* from Sandelzhausen and Steinheim a. A. in comparison to other rhino taxa, and therefore assumed feeding in more open environment for the species. This is well in accordance with the δ^{13}C values and the slightly higher δ^{18}O values (min: −5 ‰, mean: −4.8 ‰, max: −4.2 ‰) in comparison to other taxa observed in *Lartetotherium sansaniense* from the Gratkorn locality. Comparing different values for Miocene Rhinocerotidae from literature and our own measurements (Fig. 3c), it can be observed that, independently of age and climate, *Lartetotherium sansaniense* usually shows higher values for δ^{13}C and also frequently for δ^{18}O than other Rhinocerotidae. The two teleoceratini, the large rhinocerotid *Brachypotherium* from Steinheim a. A. (data from Tütken et al. 2006) and Eichkogel (own measurements) and the smaller *Prosantorhinus germanicus* from Sandelzhausen (data from Tütken and Vennemann 2009), generally display lower δ^{13}C values. The high δ^{13}C values for *Brachypotherium* (?) from Trössing could also be explained by a wrong taxonomic identification of the specimen, as it comprises only fragments which cannot be identified with certainty. Aceratini (*Plesiaceratherium fahlbuschi*, *Hoploaceratherium* sp., *Aceratherium* ssp. (including *Alicornops simorrense*); Fig. 3c; data from Tütken et al. 2006; Tütken and Vennemann 2009; own measurements) display values inbetween the other two groups. Though we are well aware that more data are needed to reconstruct ecological adaptations for the different rhinocerotid genera and species, the data presented here already indicate different ecological niches with *Brachypotherium* and other teleoceratini feeding in a more closed mesic/woodland environment (also fitting well to the graviportal gait and limb shortening; Heissig 1999), while *Lartetotherium sansaniense* was feeding in more open environment and aceratini occupied niches inbetween, which is also well in accordance with other considerations on the ecology of the different taxa (Heissig 1999; Bentaleb et al. 2006; Tütken and Vennemann 2009).

Since serial sampling of rhinocerotid teeth has proved to be an indicator for seasonal variability (MacFadden and Higgins 2004; Zin-Maung-Maung-Thein et al. 2011), the fragmented lower second molar (m2) was sampled along the axis of the tooth from the base of enamel to occlusal surface (height about 2 cm; Fig. 4a). Unfortunately, both intra-tooth ranges, $\Delta^{13}C$ (0.5) and $\Delta^{18}O$ (0.8), are too small to infer any seasonality and $^{87}Sr/^{86}Sr$ values do not show any significant variations. Since a clear seasonality for the region around Gratkorn is indicated by sedimentology and ectothermic vertebrates (Gross et al. 2011), and by serial measurements on *Deinotherium levius* vel *giganteum* (see discussion below), the height of the tooth fragment might be too short to represent a time interval recording seasonal variation.

Proboscidea

Deinotherium levius vel *giganteum*

Values for $\delta^{13}C$ for *Deinotherium levius* vel *giganteum* are the most negative among the large mammals from Gratkorn (min: −14 ‰, mean: −13.8 ‰, max: −13.6 ‰), but are still clearly in the range for a C_3-dominated mesic/woodland environment. $\delta^{18}O$ values are generally higher (min: −5.8 ‰, mean: −4.8 ‰, max: −4.1 ‰) than for the cervid *Euprox furcatus*, but overlap more with *Listriodon splendens* and *Dorcatherium naui*. The data fit well with browsing on top canopy leaves (Bocherens and Sen 1998).

Comparing the values for $\delta^{13}C$ and $\delta^{18}O$ of *Deinotherium levius* vel *giganteum* from Gratkorn with other measurements on Proboscidea from different Miocene localities of different stratigraphic levels (see “Material” for details), it can be observed that they nest well among the deinotheriidae (Fig. 3d), which generally show values typical for browsing in a C_3 dominated mesic/woodland environment. Only one deinothere from Bruck an der Leitha (Austria, early Sarmatian) displayed higher $\delta^{13}C$ values, which could result from feeding in a more open environment. In contrast, Gomphotheres (data from Tütken and Vennemann 2009; Domingo et al. 2009, 2012) usually show higher $\delta^{13}C$ values, indicating a higher degree of mixed feeding and feeding in a more open environment, though still in C_3-dominated vegetation. Harris (1996) also described strict feeding on C_3 vegetation for African deinotheres through their evolutionary history, while other proboscideans like gomphotheres switched from C_3 to C_4 during the Late Miocene (Harris 1996; Huttunen 2000; Lister 2013). Although this change seems not to have taken place in Europe (Domingo et al. 2013), clearly different ecological niches for deinotheres (browsing in mesic/woodland environment) and gomphotheres (mixed feeding in more open environment) can be observed, fitting well to the lophodont Tapir-like dentition in deinotheres in contrast to a more bunodont dentition in gomphotheres.

Along the axis of two fragmented teeth, a series of samples was measured for $\delta^{18}O$ and $\delta^{13}C$ to check for seasonal variation (Fig. 4b). The teeth are a lower fourth premolar (p4; at least 3/4 of the original tooth crown height preserved) and a fragment of an unidentified molar (Mx/mx; at least 1/2 of the original tooth crown height preserved; due to enamel thickness, affiliation to a premolar is less likely). From general taphonomy (Aiglstorfer et al. 2014a, this issue; Havlik et al. 2014, this issue), finding position, and preservation of the two teeth, they most likely belong to one individual. However, since the tooth position of the molar cannot be determined, the sequence of mineralisation and eruption of the two teeth cannot be given. As tooth formation in the genus *Deinotherium* extends over at least 1.5 years (Macho et al. 2003), a record of at least two seasons was expected for each tooth. $\delta^{13}C$ values are quite constant and show little variation [intra-tooth range: $\Delta^{13}C$ (p4)=0.4; $\Delta^{13}C$ (Mx/mx)=0.4]. In contrast, both teeth (Fig. 4b) exhibit one clear maximum (p4: −4.1 ‰, Mx/mx: −4.1 ‰) and one clear minimum (p4: −5.8 ‰, mx/Mx: −5.7 ‰) each for $\delta^{18}O$ and intra-tooth ranges of 1.7 [$\Delta^{18}O$ (p4)] and 1.6 [$\Delta^{18}O$ (Mx/mx)].

Similar variations in $\delta^{13}C$, were observed in plant material from two localities in North America, comprising one cold desert biome (MAT 8 °C; MAP 290 mm; main precipitation in winter, spring/autumn) and one desert scrub to grassland (MAT 17 °C; MAP 300 mm; main precipitation in summer) and attributed to water stress and senescent leaves of plants by Hoppe et al. (2004). Considering additional dampening of diet $\delta^{13}C$ values due to enamel maturation in herbivores (Passey and Cerling 2002), seasonality in $\delta^{13}C$ values of the diet could thus be expected. Unfortunately, the $\delta^{13}C$ values display no clear seasonal pattern and are not concordant with the stronger and seasonal variation of $\delta^{18}O$, implying no seasonal diet change for *Deinotherium levius* vel *giganteum* but would fit to a more generalistic and unselective feeding strategy (Tütken and Vennemann 2009). However, the generally quite low $\delta^{13}C$ values point to an exclusively browsing diet. In order to ascertain if $\delta^{18}O$ variation was induced by seasonality of the local climate or seasonal migration of the animal, $^{87}Sr/^{86}Sr$ measurements were accomplished on the samples displaying maxima and minima for $\delta^{18}O$. Though $^{87}Sr/^{86}Sr$ values differ distinctly from the local fauna (see discussion below), no significant intra-tooth variation could be observed and thus $\delta^{18}O$ variation more likely represents seasonality than extensive migration of the animal at the time of enamel mineralisation. As each tooth displays one maximum (summer) and one minimum (winter), a 1-year cycle would be recorded by combining the two patterns, under the assumption that both teeth belong to the same individual.

Provenance analysis ($^{87}Sr/^{86}Sr$)

As mentioned above, $^{87}Sr/^{86}Sr$ values of fossil bones and teeth are useful to detect the provenance of different faunal elements in a taphocoenosis. Small mammals as well as invertebrates more likely represent the locally bioavailable $^{87}Sr/^{86}Sr$ ratio (Hoppe

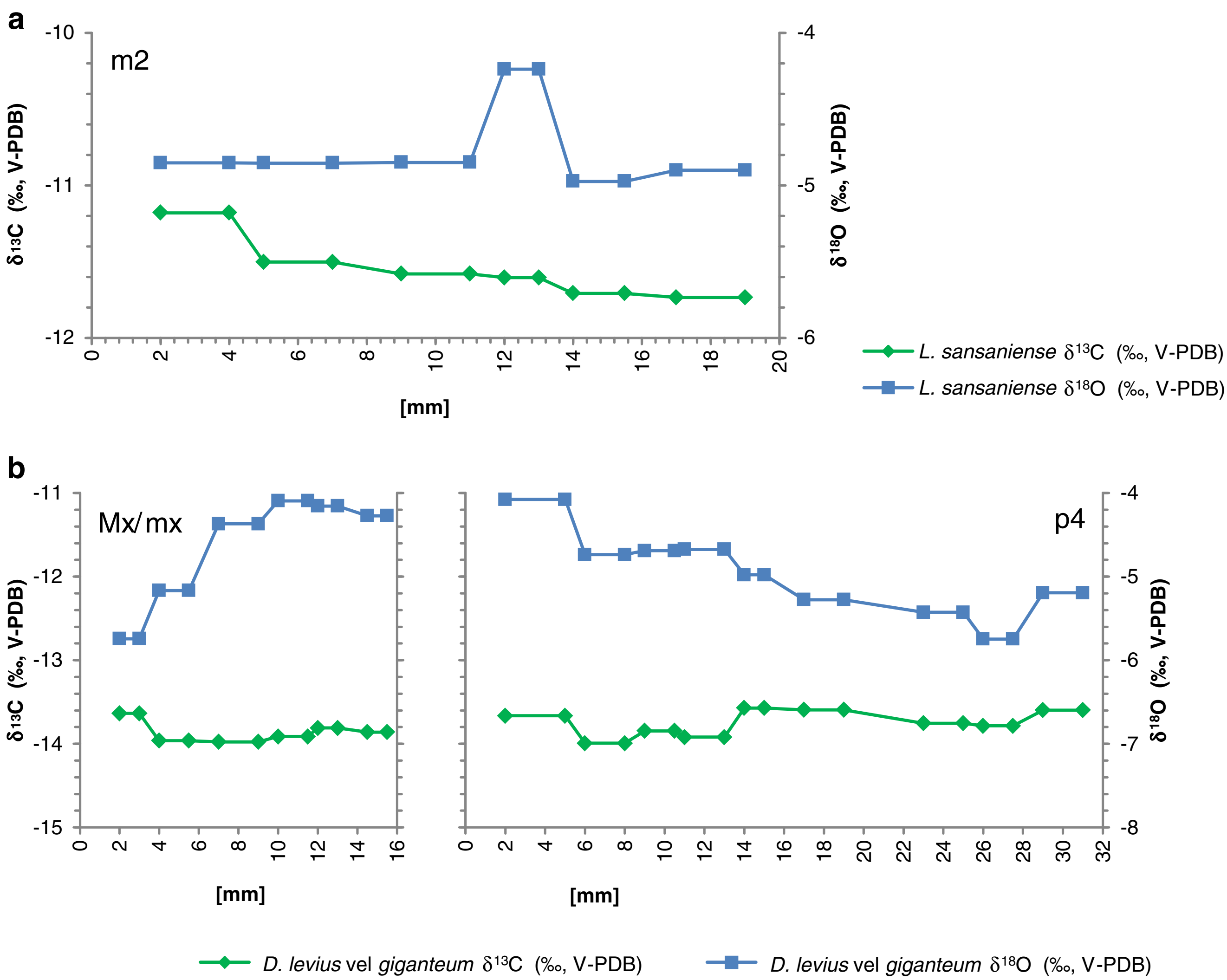

Fig. 4 Serial values of $\delta^{13}C$ (‰ V-PDB) and $\delta^{18}O_{CO3}$ (‰ V-PDB) along the tooth crown axis from base (0 mm) to occlusal surface of the lower second molar of *Lartetotherium sansaniense* from Gratkorn (**a**), and of the unidentified molar and the lower fourth premolar of *Deinotherium levius* vel *giganteum* from Gratkorn (**b**)

et al. 1999; Bentley 2006; Tütken and Vennemann 2009; Maurer et al. 2012). Although Maurer et al. (2012) observed that modern snail shells can be biased concerning the locally bioavailable $^{87}Sr/^{86}Sr$ ratio, at Gratkorn they are well in accordance with the small mammals and the microbialite, and thus represent the local signal, which is on average 0.711232 and ranges from 0.711031 to 0.711366 (Fig. 5). Among the large mammals, only *Tethytragus* sp. ($^{87}Sr/^{86}Sr$: 0.711472) and *Dorcatherium naui* ($^{87}Sr/^{86}Sr$: 0.711261) did not show significant differences from the local ratio and are interpreted as more or less permanent residents of the area around Gratkorn. Although small mammal samples suffered from a considerable diagenetic overprint, we still consider their $^{87}Sr/^{86}Sr$ ratio as a local signal of the Gratkorn locality representative for the time of sediment deposition (including early diagenesis). Small mammals, microbialite, gastropods, *Tethytragus* sp. and *Dorcatherium naui* are well in agreement concerning their $^{87}Sr/^{86}Sr$ ratios. It could be argued that the sample of *Tethytragus* sp. with its high REE content might also have been influenced by diagenesis. However, its $\delta^{18}O$ and $\delta^{13}C$ values are not shifted in the direction of the small mammals, as would be expected in a case of strong alteration. Furthermore, the non-recrystallised gastropod, *Pleurodonte michalkovaci*, and the sample of *Dorcatherium naui*, are less likely to be considerably influenced by diagenesis (as mentioned above) and show similar values for $^{87}Sr/^{86}Sr$.

The suid *Listriodon splendens* (0.710888) and the rhinocerotid *Lartetotherium sansaniense* (mean $^{87}Sr/^{86}Sr$=0.710633) showed slightly lower values, while $^{87}Sr/^{86}Sr$ values for *Euprox furcatus* ($^{87}Sr/^{86}Sr$=0.710249) and *Deinotherium levius* vel *giganteum* (mean $^{87}Sr/^{86}Sr$ (p4)=0.709271 and mean $^{87}Sr/^{86}Sr$ (Mx/mx)= 0.709234) are considerably shifted to lower values. These taxa ingested food and water in areas where $^{87}Sr/^{86}Sr$ ratios of bioavailable strontium were lower. The values are shifted in the direction of marine carbonates (Fig. 5), which in general show values from 0.7076 to 0.7092 depending on the composition of the sea water and the age (McArthur et al. 2001; Tütken 2010). Increased total Sr content (Appendix 1) in contrast to other species might have biased the $^{87}Sr/^{86}Sr$ value for *Deinotherium levius* vel *giganteum* to a certain degree, but as no correlation can be observed between $^{87}Sr/^{86}Sr$ values and Sr content, taking into consideration the other large mammals, the decreased value for *Deinotherium levius* vel *giganteum* is still considered reliable, but treated with caution. $^{87}Sr/^{86}Sr$ values for Badenian to early Sarmatian (16–12.2 Ma) marine shark teeth and foraminifera from the nearby shallow marine Vienna Basin showed values from 0.708741 to 0.708893 (Hagmaier 2002; Kocsis et al. 2009), while late Karpatian to early Badenian localities from the more open Pannonian basin showed values of 0.708814 and 0.708895 (Kocsis et al. 2009). The Gratkorn locality is located in a satellite basin of the Styrian basin (Gross et al. 2011). As the latter was connected to both the more open Pannonian Basin and the shallower Vienna Basin during marine sedimentation in Badenian and early Sarmatian times, similar values are thus expected for the Styrian Basin. Due to a marginal marine situation at this time for the area south of Gratkorn, an enhanced terrestrial clastic sediment input could have shifted the normal marine ratios to higher values. A terrestrial influence is documented by early Sarmatian marine pelites with intercalated gravels and sands in a drill core less than 20 km south of Gratkorn (Gross et al. 2007). Thus, *Euprox furcatus* and occasionally also *Listriodon splendens* and *Lartetotherium sansaniense* could have ingested food and water in areas where bioavailable $^{87}Sr/^{86}Sr$ resulted from these underlying bedrocks, while *Deinotherium levius* vel *giganteum* could have inhabited areas in the Styrian Basin with underlying marine sediments showing less terrestrial input.

In contrast to all other species, $^{87}Sr/^{86}Sr$ values (0.712732) for *Parachleuastochoerus steinheimensis* are distinctly higher than the local mean. Therefore, a different habitat is assumed for this species, with bedrocks yielding much higher $^{87}Sr/^{86}Sr$ values in bioavailable strontium than can be observed in Gratkorn. The Gratkorn locality is in close vicinity to the Eastern Alpine Mountain Chain, which consists to a considerable extent of Palaeozoic felsic magmatites and metamorphites. Palaeozoic granites and mica schists display higher $^{87}Sr/^{86}Sr$ values (Bentley 2006; Tütken 2010) and thus could be a possible bedrock for the habitat of *Parachleuastochoerus steinheimensis.*

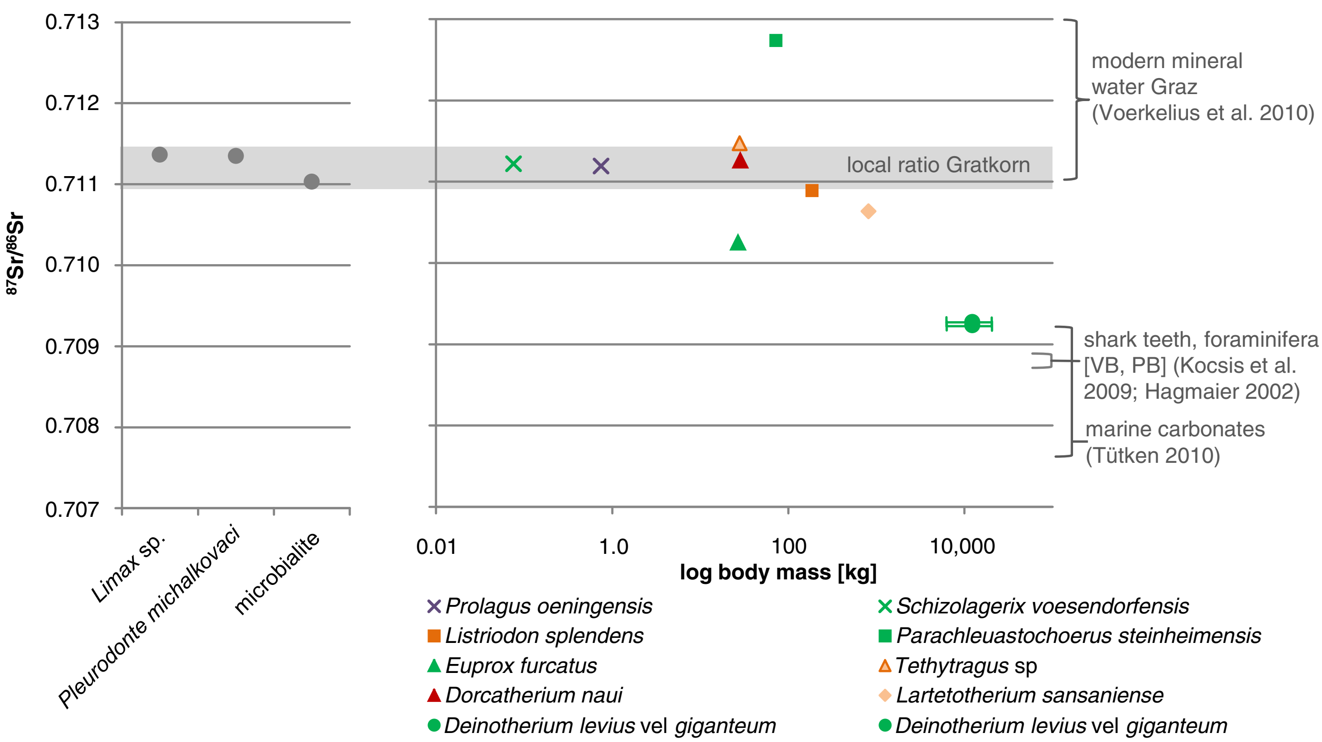

Fig. 5 $^{87}Sr/^{86}Sr$ isotope compositions from Gratkorn versus body mass (mammals only). Gastropods, the microbialite and small mammals (complete teeth) represent the local ratio for the locality. Most of the large mammals (enamel), especially with larger body mass, show different values from the local ratio due to migration (maybe provoked by limitation of available biomass at the locality). The values are compared to the modern natural mineral water values from Graz (data from Voerkelius et al. 2010), to the range for marine carbonates in general (data from Tütken 2010) and to ratios from measurements on shark teeth and foraminifera from late Karpatian to early Sarmatian sediments from Austria (Bad Vöslau, Leithakalk, Siebenhirten) and Hungary (Danitzpuszta and Himesháza) (data from Kocsis et al. 2009; Hagmaier 2002; *VB* Vienna Basin; *PB* Pannonian Basin). Bodymass estimations follow Aiglstorfer et al. (2014c, this issue) for ruminants; Costeur et al. (2012) for *Listriodon splendens* and *Prolagus oeningensis*; Aiglstorfer et al. (2014a, this issue, and citations therein) for *Deinotherium levius* vel *giganteum*; and Fortelius (2013 (NOW database)) for *Parachleuastochoerus steinheimensis*; and is oriented for *Schizogalerix voesendorfensis* on the value for *Schizogalerix* sp. given by Merceron et al. (2012)

Summing up, no detailed migrational history can be reconstructed from $^{87}Sr/^{86}Sr$ ratios of the large mammals from Gratkorn due to limited data. However, it can be observed that, besides the more or less local residents *Tethytragus* sp. and *Dorcatherium naui*, the other large mammals, *Listriodon splendens* (only to a minor degree), *Lartetotherium sansaniense*, *Euprox furcatus*, *Deinotherium levius* vel *giganteum*, and *Parachleuastochoerus steinheimensis*, lived in areas with lower or higher $^{87}Sr/^{86}Sr$ ratios in bioavailable strontium, at least temporarily. Especially the larger herbivores, such as the proboscidean or the rhinocerotids (see Fig. 5 for bodymasses), were dependent on a large amount of daily food supply. A limitation in available biomass (at least during some seasons) at the Gratkorn locality might be an explanation for migration of the larger mammals. However, for small mammals and the maybe better adapted *Dorcatherium naui* and *Tethytragus* sp., food supply could have been enough during all seasons. With slightly higher values, the latter might have occasionally fed on bedrocks with higher values as well.

Conclusions

In summary, the herbivorous large mammals from Gratkorn were feeding on an exclusively C_3 vegetation and predominantly browsing in mesic/woodland environments. The isotope data of large mammal enamel presented here (for some taxa, comprising the first isotope data so far) indicate occupation of different ecological niches. Since the data from Gratkorn are well in accordance with measurements from other Miocene localities from different stratigraphic levels and with different climatic conditions (Tütken et al. 2006; Domingo et al. 2009, 2012; Tütken and Vennemann 2009,) relatively stable ecological niches can be reconstructed for some taxa.

Significantly higher $\delta^{13}C$ values in *Dorcatherium naui* than displayed by the rest of the large mammal fauna from Gratkorn point to an ingestion of more fruits in its diet. The small moschid *Micromeryx flourensianus* could also have ingested fruits from time to time. The cervid *Euprox furcatus* represents a typical subcanopy browser and thus preferably occupied a different niche than the cervid *Heteroprox* (not recorded at Gratkorn), which was more adapted to an open environment. In spite of its small size, the bovid *Tethytragus* sp. represents a canopy browser (with a possibly caprine-like postcranial adaptation). The proboscidean *Deinotherium levius* vel *giganteum* browsed on canopy plants in the higher parts of an exclusively C_3 vegetation, in contrast to the more bunodont proboscidean *Gomphotherium*, which has not so far been recorded from Gratkorn, and exhibited a more mixed feeding diet. The latter proboscidean genus is recorded for Austria at the time of the Gratkorn locality. Its absence from the mammal assemblage from Gratkorn could thus have ecological reasons. Generally higher values for $\delta^{18}O$ and $\delta^{13}C$ in *Lartetotherium sansaniense* indicate feeding in more open environments, as has also been observed for other localities (Tütken et al. 2006; Tütken and Vennemann 2009). *Listriodon splendens* was a typical browsing taxon with considerable input of fruits and maybe some grass in its diet, while the other suid from Gratkorn, *Parachleuastochoerus steinheimensis*, showed a certain degree of rooting as part of its diet. These different ecological niches for Listriodontinae and Tetraconodontinae seem to be quite stable, as similar values can be observed for different localities with different stratigraphic ages. Serial measurements on the teeth of *Deinotherium levius* vel *giganteum* show a seasonal variation at this time for the wider area around Gratkorn, fitting well to sedimentology and climate reconstructions based on ectothermic vertebrates from the Gratkorn locality itself (Gross et al. 2011; Böhme and Vasilyan 2014, this issue). Distinct differences in $^{87}Sr/^{86}Sr$ values indicate that not all large mammals were permanent residents of the area around Gratkorn, but inhabited a wider area, most likely including the Styrian Basin and the palaeozoic and metamorphic basement in the Eastern Alps. Biomass at the locality itself was most likely limited, and thus maybe not enough food was available for the largest herbivores during all seasons. Therefore, it can be assumed that the largest mammals were migrating to a certain degree.

We can reconstruct for the wider area around the Gratkorn locality an ecosystem with predominantly C_3 vegetation in a semi-arid, subtropical climate with distinct seasonality and too little precipitation for a closed canopy woodland. It provided enough diversity in plant resources to allow occupation of different niches, from subcanopy browsing and rooting to top canopy browsing, plus a certain degree of frugivory and mixed feeding for diverse large mammals. This or similar organisation patterns can be observed in other European Miocene localities (Tütken et al. 2006; Tütken and Vennemann 2009; Domingo et al. 2009, 2012), and seem to be affected only to a minor degree by climatic conditions but rather represent a typical niche partitioning of large mammals in a Middle Miocene ecosystem.

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Appendix 1 Data from the Gratkorn locality

Table 1 $\delta^{13}C$ V-PDB (‰), $\delta^{18}O_{CO3}$ V-PDB (‰) and $\delta^{18}O_{CO3}$ V-SMOW (‰), $CaCO_3$ content (wt %), $^{87}Sr/^{86}Sr$ ratio of tooth enamel, dentine, and bone samples of small and large mammals and of invertebrates and soil samples from the Gratkorn locality

Sample	Specimen	Species	Tooth position	Tissue	$\delta^{13}C$ V-PDB (‰)	$\delta^{18}O$ V-PDB (‰)	$\delta^{18}O$ V-SMOW (‰)	$CaCO_3$ (wt. %)	$^{87}Sr/^{86}Sr$	SD	Sr content (ppm) from Havlik et al., this issue
MA- 1e	UMJGP 203427	*Listriodon splendens*	m3	Enamel	−12.4	−5.8	24.9	3.52			
MA- 312	GPIT/MA/ 02757	*Listriodon splendens*	M3	Enamel	−11.4	−2.6	28.2	3.48	0.710888000	0.000009	168
MA- 2e	UMJGP 204652	*Parachleuastochoerus steinheimensis*	m3	Enamel	−11.4	−7.9	22.7	3.12			
MA- 332	UMJGP 204652	*Parachleuastochoerus steinheimensis*	m3	Enamel					0.712732000	0.000010	
MA- 5e	UMJGP 204665	*Dorcatherium naui*	m3	Enamel	−11.3	−4.0	26.7	3.32			
MA- 6e	UMJGP 204662	*Dorcatherium naui*	m3	Enamel	−11.3	−5.2	25.6	2.03			
MA- 7e	UMJGP 204109	*Dorcatherium naui*	m3	Enamel	−11.8	−5.0	25.7	4.60	0.711261000	0.000010	227
MA- 88	UMJGP 210694	*Dorcatherium naui*	m3	Enamel	−5.2	−5.4	25.3	3.58			
MA- 3e	UMJGP 204711	*Euprox furcatus*	m3	Enamel	−13.3	−7.7	22.9	4.30	0.710249000	0.000009	313
MA- 4e	UMJGP 204713	*Euprox furcatus*	m3	Enamel	−13.5	−7.4	23.2	3.00			
MA- 308	GPIT/MA/2386	*Euprox furcatus*	m3	Enamel	−12.0	−6.4	24.3	3.95			
MA- 314	GPIT/MA/ 02739	*Euprox furcatus*	M3	Enamel	−13.6	−5.0	25.8	3.09			
MA- 317	GPIT/MA/ 02393	*Euprox furcatus*	m3	Enamel	−12.3	−6.9	23.8	4.25			
MA- 89	UMJGP 204685	*Micromeryx flourensianus*	m3	Enamel	−12.3	−5.4	25.3	4.43			
MA- 325	GPIT/MA/ 02753	*Tethytragus* sp.	M2?	Enamel	−13.1	−1.7	29.1	4.79	0.711472000	0.000009	145
MA- 67	UMJGP 203459	*Lartetotherium sansaniense*	m2 - base	Enamel	−11.2	−4.9	25.9	3.63	0.710517000	0.000009	136 (measured on fragment of tooth)
MA- 68	UMJGP 203459	*Lartetotherium sansaniense*	m2 - 2	Enamel	−11.5	−4.9	25.9	2.30			
MA- 69	UMJGP 203459	*Lartetotherium sansaniense*	m2 - 3	Enamel	−11.6	−4.8	25.9	2.71			
MA- 70	UMJGP 203459	*Lartetotherium sansaniense*	m2 - 4	Enamel	−11.6	−4.2	26.5	2.95	0.710700000	0.000009	
MA- 71	UMJGP 203459	*Lartetotherium sansaniense*	m2 - 5	Enamel	−11.7	−5.0	25.7	2.01			
MA- 72	UMJGP 203459	*Lartetotherium sansaniense*	m2 - tip	Enamel	−11.7	−4.9	25.8	2.29	0.710684000	0.000009	
MA- 73	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx - base	Enamel	−13.6	−5.7	24.9	4.28	0.709233000	0.000010	
MA- 74	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx-2	Enamel	−14.0	−5.2	25.5	3.76			
MA- 75	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx-3	Enamel	−14.0	−4.4	26.4	3.67			

Table 1 (continued)

Sample	Specimen	Species	Tooth position	Tissue	$\delta^{13}C$ V-PDB (‰)	$\delta^{18}O$ V-PDB (‰)	$\delta^{18}O$ V-SMOW (‰)	$CaCO_3$ (wt. %)	$^{87}Sr/^{86}Sr$	SD	Sr content (ppm) from Havlik et al., this issue
MA- 76	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx-4	Enamel	−13.9	−4.1	26.6	3.64	0.709222000	0.000012	
MA- 77	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx-5	Enamel	−13.8	−4.2	26.6	2.32			
MA- 78	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx - tip	Enamel	−13.9	−4.3	26.5	2.38	0.709247000	0.000009	
MA- 79	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - base	Enamel	−13.7	−4.1	26.7	2.77	0.709277000	0.000010	2,536 (measured on fragment of tooth)
MA- 80	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 2	Enamel	−14.0	−4.7	26.0	2.31			
MA- 81	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 3	Enamel	−13.8	−4.7	26.0	3.29			
MA- 82	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 4	Enamel	−13.9	−4.7	26.0	3.36			
MA- 83	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 5	Enamel	−13.6	−5.0	25.7	3.75	0.709262000	0.000011	
MA- 84	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 6	Enamel	−13.6	−5.3	25.4	3.78			
MA- 85	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 7	Enamel	−13.8	−5.4	25.3	2.35			
MA- 86	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - 8	Enamel	−13.8	−5.8	24.9	2.20	0.709276000	0.000009	
MA- 87	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4 - tip	Enamel	−13.6	−5.2	25.5	2.72			
MA- 323	No number	*Schizogalerix voesendorfensis*	Cheek teeth	Dentine/enamel	−8.5	−5.1	25.6	4.58	0.711218000	0.000009	
MA- 324	No number	*Prolagus oeningensis*	Cheek teeth	Dentine/enamel	−9.9	−5.7	25.0	4.70	0.711193000	0.000010	
MA- 327	No number	Undetermined small mammal	Incisor	Dentine/enamel	−8.3	−7.1	23.5	5.47			
MA- 178	No number	*Pseudidyla martingrossi*		Shell	−7.7	−2.4	28.4	98.96			
MA- 179	No number	*Limax* sp.		Shell	−7.0	−2.6	28.1	92.52	0.711366000	0.000024	
MA- 180	No number	*Pleurodonte michalkovaci*		Shell	−7.3	−3.0	27.8	101.12	0.711350000	0.000009	
MA- 182	No number	*Testacella schuetti*		Shell	−7.1	−4.9	25.8	95.41			
MA- 183	No number	Operculum of indetermined gastropoda			−5.3	−6.6	24.0	100.63			
MA- 176	No number	*Celtis* sp.		Endocarb	−7.3	3.7	34.8	97.35			
MA- 177	No number	*Celtis* sp.		Endocarb	−10.0	2.5	33.5	97.35			
MA- 320	No number	Microbialite		Carbonate	−12.6	−7.6	23.0	85.24	0.711031000	0.000011	
MA- 307	From UMJGP 210694	Sediment		Sediment	−1.2	−5.6	25.1	0.46			

Table 1 (continued)

Sample	Specimen	Species	Tooth position	Tissue	$\delta^{13}C$ V-PDB (‰)	$\delta^{18}O$ V-PDB (‰)	$\delta^{18}O$ V-SMOW (‰)	$CaCO_3$ (wt. %)	$^{87}Sr/^{86}Sr$	SD	Sr content (ppm) from Havlik et al., this issue
MA- 311	From GPIT/MA/ 2386	Sediment		Sediment	−9.5	−7.6	23.1	0.16			
MA- 316	From GPIT/MA/ 02739	Sediment		Sediment	−14.0	−9.4	21.1	0.13			
MA- 321	From G 105/12	Soil upper part/leave		Sediment	−7.7	−7.2	23.4	0.08			
MA- 322	From GPIT/MA/ 02757	Soil lower part		Sediment	−20.9	−11.1	19.4	0.23			
MA- 1w	UMJGP 203427	*Listriodon splendens*	m3 root	Dentine	−7.2	−5.6	25.1	5.91			
MA- 2 k	UMJGP 204652	*Parachleuastochoerus steinheimensis*	Dentary	Bone	−9.2	−7.0	23.7	5.46			
MA- 5w	UMJGP 204665	*Dorcatherium naui*	m3 root	Dentine	−8.7	−5.8	24.8	6.60			
MA- 5 k	UMJGP 204665	*Dorcatherium naui*	Dentary	Bone	−8.5	−5.8	24.9	7.14			
MA- 6w	UMJGP 204662	*Dorcatherium naui*	m3 root	Dentine	−8.8	−5.5	25.1	3.91			
MA- 6 k	UMJGP 204662	*Dorcatherium naui*	Dentary	Bone	−8.5	−5.8	24.9	6.90			
MA- 168	UMJGP 204109	*Dorcatherium naui*	m2 root	Dentine	−7.9	−5.9	24.8	4.05			
MA- 306	UMJGP 210694	*Dorcatherium naui*	m3 root	Dentine	−6.3	−6.0	24.7	4.47			
MA- 4w	UMJGP 204713	*Euprox furcatus*	m3 root	Dntine	−9.3	−5.5	25.2	6.33			
MA- 167	UMJGP 204711	*Euprox furcatus*	m3 root	Dentine	−9.1	−5.6	25.1	5.26			
MA- 328	UMJGP 204685	*Micromeryx flourensianus*	Dentary	Bone	−8.8	−5.3	25.4	5.90			
MA- 169	UMJGP 203459	*Lartetotherium sansaniense*	m2	Dentine	−6.9	−5.6	25.1	4.98			
MA- 170	UMJGP 203435	*Deinotherium levius* vel *giganteum*	p4	Dentine	−7.8	−6.1	24.6	5.63			
MA- 171	UMJGP 203421	*Deinotherium levius* vel *giganteum*	Mx/mx	Dentine	−8.0	−6.0	24.7	5.13	0.710284000	0.000010	
MA- 313	GPIT/MA/ 02757	*Listriodon splendens*	M3	Dentine	−7.7	−4.8	25.9	4.33			
MA- 315	GPIT/MA/ 02739	*Euprox furcatus*	Maxilla	Bone	−7.7	−5.0	25.7	4.83			
MA- 319	GPIT/MA/ 02393	*Euprox furcatus*	Dentary	Bone	−8.7	−5.5	25.2	4.20			
MA- 326	GPIT/MA/ 02753	*Tethytragus* sp.	M2?	Dentine	−8.3	−4.5	26.2	4.69			

Appendix 2 Comparison data from Austrian localities

Table 2 $\delta^{13}C$ V-PDB (‰), $\delta^{18}O_{CO3}$ V-PDB (‰) and $\delta^{18}O_{CO3}$ V-SMOW (‰) values and $CaCO_3$ content (wt %) of tooth enamel, dentine, and bone samples of large mammals from several Austrian localities used as comparison data

Sample	Specimen	Species	Tooth position	Tissue	$\delta^{13}C$ V-PDB (‰)	$\delta^{18}O$ V-PDB (‰)	$\delta^{18}O$ V-SMOW (‰)	$CaCO_3$ (wt. %)	Kind of site	Age (Ma)	Locality
MA- 8	IGM 6025	*Dorcatherium crassum*	m3	Enamel	−9.6	−9.0	21.6	3.31	Intramontane	~14.5	Göriach
MA- 27	UMJGP 1942	*Dorcatherium crassum*	m3	Enamel	−8.3	−6.4	24.2	2.12	Intramontane	~14.5	Göriach
MA- 28	UMJGP 3787	*Dorcatherium crassum*	m3	Enamel	−7.6	−5.3	25.4	2.31	Intramontane	~14.5	Göriach
MA- 287	UMJGP 1952	*Dorcatherium crassum*	m3	Enamel	−10.6	−8.9	21.7	3.88	Intramontane	~14.5	Göriach
MA- 30	UMJGP 1918	*Dorcatherium vindebonense*	m3	Enamel	−6.9	−5.4	25.3	3.05	Intramontane	~14.5	Göriach
MA- 288	UMJGP 56886	*Heteroprox larteti*	M3	Enamel	−11.5	−5.0	25.7	2.85	Intramontane	14.8	Seegraben
MA- 9	IGM 89	*Prodeinotherium bavaricum*	Mx/mx - base	Enamel	−13.8	−7.5	23.1	4.21	Intramontane	14.8	Seegraben
MA- 10	IGM 89	*Prodeinotherium bavaricum*	Mx/mx-2	Enamel	−13.3	−5.7	24.9	2.76	Intramontane	14.8	Seegraben
MA- 11	IGM 89	*Prodeinotherium bavaricum*	Mx/mx-3	Enamel	−13.1	−6.7	24.0	2.70	Intramontane	14.8	Seegraben
MA- 12	IGM 89	*Prodeinotherium bavaricum*	Mx/mx-4	Enamel	−13.0	−7.1	23.5	2.56	Intramontane	14.8	Seegraben
MA- 13	IGM 89	*Prodeinotherium bavaricum*	Mx/mx-5	Enamel	−13.7	−7.9	22.8	3.56	Intramontane	14.8	Seegraben
MA- 14	IGM 89	*Prodeinotherium bavaricum*	Mx/mx-6	Enamel	−13.1	−6.3	24.4	4.03	Intramontane	14.8	Seegraben
MA- 15	IGM 89	*Prodeinotherium bavaricum*	Mx/mx - tip	Enamel	−13.1	−6.8	23.9	4.18	Intramontane	14.8	Seegraben
MA- 226	NHMW 1872 V 11	*Deinotherium* sp.	Px - base	Enamel	−12.8	−5.9	24.8	3.59	Vienna Basin	12.6	Türkenschanze
MA- 227	NHMW 1872 V 11	*Deinotherium* sp.	Px-2	Enamel	−13.0	−5.8	24.9	3.39	Vienna Basin	12.6	Türkenschanze
MA- 228	NHMW 1872 V 11	*Deinotherium* sp.	Px-3	Enamel	−13.0	−5.7	24.9	3.37	Vienna Basin	12.6	Türkenschanze
MA- 229	NHMW 1872 V 11	*Deinotherium* sp.	Px-4	Enamel	−12.8	−5.3	25.4	3.32	Vienna Basin	12.6	Türkenschanze
MA- 230	NHMW 1872 V 11	*Deinotherium* sp.	Px-5	Enamel	−13.1	−6.5	24.2	2.95	Vienna Basin	12.6	Türkenschanze
MA- 231	NHMW 1872 V 11	*Deinotherium* sp.	Px-6	Enamel	−12.6	−5.8	24.9	3.11	Vienna Basin	12.6	Türkenschanze
MA- 232	NHMW 1872 V 11	*Deinotherium* sp.	Px - tip	Enamel	−12.7	−5.6	25.1	3.08	Vienna Basin	12.6	Türkenschanze
MA- 95	UMJGP 50165	*Deinotherium* sp.	Mx/mx - base	Enamel	−11.5	−4.3	26.4	3.30	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 96	UMJGP 50165	*Deinotherium* sp.	Mx/mx-2	Enamel	−11.5	−3.9	26.8	2.99	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 97	UMJGP 50165	*Deinotherium* sp.	Mx/mx-3	Enamel	−11.8	−4.3	26.5	2.82	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 98	UMJGP 50165	*Deinotherium* sp.	Mx/mx-4	Enamel	−11.8	−5.2	25.5	2.73	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 99	UMJGP 50165	*Deinotherium* sp.	Mx/mx-5	Enamel	−11.7	−5.5	25.2	3.06	Styrian Basin	12.7–11.10	Trössing near Gnas
MA- 100	UMJGP 50165	*Deinotherium* sp.	Mx/mx-6	Enamel	−11.6	−5.6	25.1	3.02	Styrian Basin	12.7–11.10	Trössing near Gnas

Table 2 (continued)

Sample	Specimen	Species	Tooth position	Tissue	$\delta^{13}C$ V-PDB (‰)	$\delta^{18}O$ V-PDB (‰)	$\delta^{18}O$ V-SMOW (‰)	$CaCO_3$ (wt. %)	Kind of site	Age (Ma)	Locality
MA- 101	UMJGP 50165	*Deinotherium* sp.	Mx/mx-7	Enamel	−11.5	−5.2	25.5	3.17	Styrian Basin	12.7–11.10	Trössing near Gnas
MA- 102	UMJGP 50165	*Deinotherium* sp.	Mx/mx-8	Enamel	−11.5	−5.0	25.7	3.29	Styrian Basin	12.7–11.10	Trössing near Gnas
MA- 103	UMJGP 50165	*Deinotherium* sp.	Mx/mx-9	Enamel	−11.5	−5.8	24.9	3.01	Styrian Basin	12.7–11.10	Trössing near Gnas
MA- 104	UMJGP 50165	*Deinotherium* sp.	Mx/mx - tip	Enamel	−11.4	−4.7	26.0	3.66	Styrian Basin	12.7–11.10	Trössing near Gnas
MA- 215	NHMW 2000z0024/0000	*Deinotherium giganteum*	M2?	Enamel	−10.0	−5.9	24.8	3.79	Vienna Basin	12.7–12.2	Bruck a.d. Leitha
MA- 31	UMJGP 45.816	*Deinotherium giganteum*	Mx/mx - base	Enamel	−14.0	−6.2	24.5	2.83	Styrian Basin	Early Late Miocene	Wolfau
MA- 32	UMJGP 45.816	*Deinotherium giganteum*	Mx/mx-2	Enamel	−14.0	−5.7	25.0	3.03	Styrian Basin	Early Late Miocene	Wolfau
MA- 33	UMJGP 45.816	*Deinotherium giganteum*	Mx/mx-3	Enamel	−13.3	−5.1	25.6	1.63	Styrian Basin	Early Late Miocene	Wolfau
MA- 34	UMJGP 45.816	*Deinotherium giganteum*	Mx/mx-4	Enamel	−13.2	−7.5	23.1	3.48	Styrian Basin	Early Late Miocene	Wolfau
MA- 35	UMJGP 45.816	*Deinotherium giganteum*	Mx/mx-5	Enamel	−13.6	−6.1	24.5	1.65	Styrian Basin	Early Late Miocene	Wolfau
MA- 36	UMJGP 45.816	*Deinotherium giganteum*	Mx/mx - tip	Enamel	−13.6	−6.0	24.7	1.61	Styrian Basin	Early Late Miocene	Wolfau
MA- 234	NHMW 1898	*Deinotherium giganteum*	M2? - base	Enamel	−12.2	−4.8	25.9	3.17	Vienna Basin	Miocene	Mödling
MA- 235	NHMW 1898	*Deinotherium giganteum*	M2? - 2	Enamel	−11.8	−5.0	25.7	3.18	Vienna Basin	Miocene	Mödling
MA- 236	NHMW 1898	*Deinotherium giganteum*	M2? - 3	Enamel	−12.3	−6.2	24.5	3.07	Vienna Basin	Miocene	Mödling
MA- 237	NHMW 1898	*Deinotherium giganteum*	M2? - 4	Enamel	−12.0	−5.0	25.7	2.91	Vienna Basin	Miocene	Mödling
MA- 238	NHMW 1898	*Deinotherium giganteum*	M2? - 5	Enamel	−11.5	−5.2	25.5	2.78	Vienna Basin	Miocene	Mödling
MA- 239	NHMW 1898	*Deinotherium giganteum*	M2? - 6	Enamel	−11.9	−6.6	24.1	2.78	Vienna Basin	Miocene	Mödling
MA- 240	NHMW 1898	*Deinotherium giganteum*	M2? - 7	Enamel	−11.7	−6.1	24.6	2.70	Vienna Basin	Miocene	Mödling
MA- 241	NHMW 1898	*Deinotherium giganteum*	M2? - 8	Enamel	−11.4	−5.5	25.2	2.69	Vienna Basin	Miocene	Mödling
MA- 242	NHMW 1898	*Deinotherium giganteum*	M2? - 9	Enamel	−11.6	−5.2	25.5	2.81	Vienna Basin	Miocene	Mödling
MA- 243	NHMW 1898	*Deinotherium giganteum*	M2? - 10	Enamel	−11.5	−5.4	25.3	2.91	Vienna Basin	Miocene	Mödling
MA- 244	NHMW 1898	*Deinotherium giganteum*	M2? - tip	Enamel	−11.7	−5.7	25.0	3.13	Vienna Basin	Miocene	Mödling
MA- 23	IGM 3439	*Hoploaceratherium* sp.	Mx/mx - base	Enamel	−11.8	−6.7	24.0	3.42	Intramontane	~14.5	Göriach
MA- 24	IGM 3439	*Hoploaceratherium* sp.	Mx/mx-2	Enamel	−11.6	−6.7	24.0	2.67	Intramontane	~14.5	Göriach
MA- 25	IGM 3439	*Hoploaceratherium* sp.	Mx/mx-3	Enamel	−12.0	−7.8	22.8	1.95	Intramontane	~14.5	Göriach
MA- 26	IGM 3439	*Hoploaceratherium* sp.	Mx/mx - tip	Enamel	−12.5	−7.0	23.6	2.54	Intramontane	~14.5	Göriach
MA- 116	UMJGP 50178	*Brachypotherium* (?)	Mx/mx - base	Enamel	−11.9	−5.5	25.2	3.66	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 117	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-2	Enamel	−11.8	−5.5	25.2	3.22	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 118	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-3	Enamel	−11.8	−6.2	24.5	3.07	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 119	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-4	Enamel	−11.7	−6.5	24.2	2.87	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 120	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-5	Enamel	−11.6	−5.9	24.8	2.79	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 121	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-6	Enamel	−11.4	−5.9	24.8	2.87	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 122	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-7	Enamel	−11.4	−5.6	25.1	2.84	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 123	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-8	Enamel	−11.3	−5.9	24.8	2.87	Styrian Basin	12.7–11.6	Trössing near Gnas

Table 2 (continued)

Sample	Specimen	Species	Tooth position	Tissue	$\delta^{13}C$ V-PDB (‰)	$\delta^{18}O$ V-PDB (‰)	$\delta^{18}O$ V-SMOW (‰)	$CaCO_3$ (wt. %)	Kind of site	Age (Ma)	Locality
MA- 124	UMJGP 50178	*Brachypotherium* (?)	Mx/mx-9	Enamel	−11.5	−6.4	24.3	2.86	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 125	UMJGP 50178	*Brachypotherium* (?)	Mx/mx - tip	Enamel	−11.4	−6.1	24.6	3.05	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 217	NHMW 1954/74	*Brachypotherium* sp.	Mx - tip	Enamel	−12.6	−6.2	24.5	3.18	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 218	NHMW 1954/74	*Brachypotherium* sp.	Mx-2	Enamel	−12.7	−7.0	23.6	3.00	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 219	NHMW 1954/74	*Brachypotherium* sp.	Mx-3	Enamel	−12.4	−7.2	23.4	2.93	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 220	NHMW 1954/74	*Brachypotherium* sp.	Mx-4	Enamel	−12.3	−7.2	23.4	2.57	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 221	NHMW 1954/74	*Brachypotherium* sp.	Mx-5	Enamel	−12.3	−6.6	24.1	2.68	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 222	NHMW 1954/74	*Brachypotherium* sp.	Mx-6	Enamel	−12.5	−6.3	24.3	3.18	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 223	NHMW 1954/74	*Brachypotherium* sp.	Mx-7	Enamel	−12.7	−6.1	24.6	3.22	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 224	NHMW 1954/74	*Brachypotherium* sp.	Mx - base	Enamel	−12.8	−6.3	24.4	3.77	Vienna Basin	Miocene	Eichkogel near Mödling
MA- 286	UMJGP 1942	*Dorcatherium crassum*	m3 root	Dentine	−7.4	−7.5	23.1	5.78	Intramontane	~14.5	Göriach
MA- 283	UMJGP 3787	*Dorcatherium crassum*	Bone	Bone	−4.2	−7.7	22.9	6.12	Intramontane	~14.5	Göriach
MA- 285	UMJGP 1952	*Dorcatherium crassum*	m3 root	Dentine	−8.6	−7.7	22.9	5.51	Intramontane	~14.5	Göriach
MA- 284	UMJGP 56886	*Heteroprox larteti*	Bone	Bone	−11.4	−9.4	21.2	6.27	Intramontane	14.8	Seegraben
MA- 282	UMJGP 45.816	*Deinotherium*	Mx/mx	Dentine	−10.4	−7.4	23.2	5.57	Styrian Basin	Early Late Miocene	Wolfau
MA- 279	UMJGP 50165	*Deinotherium*	Mx/mx	Dentine	−11.7	−5.9	24.8	5.23	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 216	NHMW 2000z0024/ 0000	*Deinotherium* sp.	M2?	Dentine	−7.7	−5.8	24.9	5.16	Vienna Basin	12.7–12.2	Bruck a.d. Leitha
MA- 233	NHMW 1872 V 11	*Deinotherium* sp.	Px	Dentine	−11.6	−4.7	26.0	5.13	Vienna Basin	12.6	Türkenschanze
MA- 245	NHMW 1898	*Deinotherium giganteum*	M2?	Dentine	−11.9	−5.8	24.9	6.36	Vienna Basin	Miocene	Mödling
MA- 276	UMJGP 50178	*Brachypotherium* (?)	Mx/mx	Dentine	−10.4	−6.0	24.7	5.42	Styrian Basin	12.7–11.6	Trössing near Gnas
MA- 225	NHMW 1954/74	*Brachypotherium* sp.	Mx	Dentine	−12.6	−6.7	24.0	6.14	Vienna Basin	Miocene	Eichkogel near Mödling

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